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Volume 40

Edited by

G. C. AINSWORTH and S. D. GARRETT

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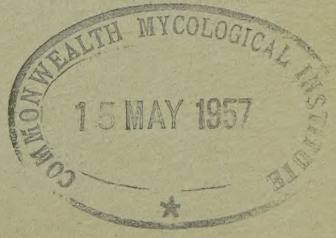

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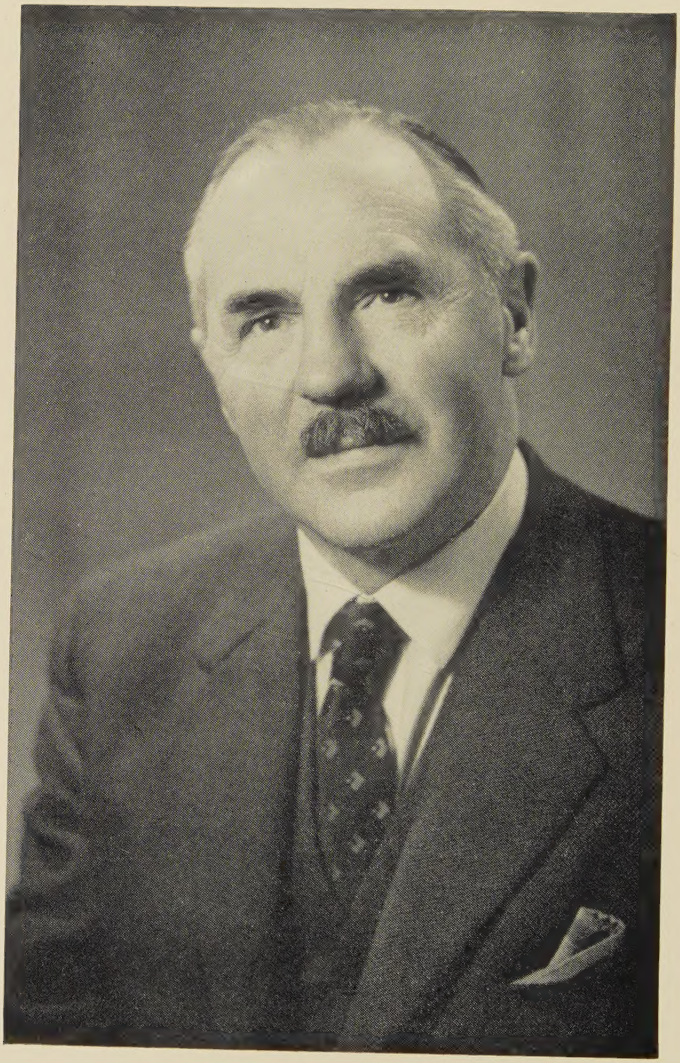

W. D. GRADDON
President, 1956

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PRESIDENTIAL ADDRESS

APPROACH TO DISCOMYCETES

By W. D. GRADDON

It is many years since the Discomycetes received other than casual mention in a presidential address to this Society. Despite their manifold attractions they have been, with little doubt, the most neglected of the fungal families. Many of them are of rare and delicate beauty; they are widespread, are to be found in plenty in every suitable habitat and have virtually no close season; by virtue of a consistency which lends itself particularly well to the rapid production of excellent sections with a freezing microtome they are rather easy to describe in great detail—although, alas, this is rarely done—and they keep extremely well as herbarium specimens—provided that they are not flattened out in piles of heavy folders as is the unfortunate practice at many important institutions.

Why then their comparative neglect? Almost the whole answer lies, I think, in the dearth of literature allowing of their easy identification. This has meant the placing upon many who have started the study of these fungi a burden of frustration too heavy to be long sustained.

In the latter half of last century they received their share of attention but following the publication, at the turn of the century, of the great works of Rehm and of Boudier came a rather dark period illuminated chiefly by the fundamental studies of von Höhnel at Vienna. The past twenty-five years has seen a lively renaissance of interest in the group and, accordingly, some consideration of them this afternoon seems opportune.

To-day I speak to you merely as one who has found much pleasure in the field work of collecting Discomycetes and in the subsequent struggles at home to identify the finds. Maybe, in the course of these efforts, I have learned to find my way a little about the labyrinth and maybe this address will provide a few sign-posts for others; I hope so.

The Discomycetes embrace ascigerous fungi with an exposed hymenium and, with only a little experience, they are as easy to recognize in the field as is implied by so simple a definition. Only sometimes are we in doubt as, for example, when on the slightly blurred boundary across which lie the Hysteriaceae or when seeing for the first time young *Hirneola auricula-judae*! Many of the lichens come within our definition but these will be left out of consideration now.

Collecting

Where and when to find Discomycetes have been admirably set out by Boudier in his *Histoire et Classification des Discomycètes d'Europe* (1907) and by Velenovsky in *Monographia Discomycetum Bohemiae* (1934); to convey to

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you the content of these surveys would take longer than I am allowed; I shall, instead, refer to some of my own preferred collecting sites and to some important—but often neglected—aspects of the art of collecting.

Collecting may, of course, be either random or directed to some particular purpose. However immersed one may become in special projects it is, I think, wise to keep going a certain amount of random collecting in order steadily to widen the field of experience. For this purpose a pleasant and productive venue is found by making one's way slowly along in the water of a small stream lightly shaded by overhanging trees—a stream such as may be found beside many a country lane. Here, in the course of a year, almost the whole range of Discomycete forms may be seen. On the damp earth banks down to the water's edge Galactinias, Scutellinias, Lamprosporas; higher up the banks amongst moss *Leotia lubrica*, *Microglossum viride* and Helvellas; on rotting wood across and in the water the brown buttons of *Psilopeziza babingtonii*, Scutellinias, *Vibrissea truncorum* with its fine golden heads, inconspicuous Apostemidiums and on overwintered twigs, leaves and stems a host of the small inoperculate species.

For more particularized hunting I recommend concentration on good colonies of a single host. It is not always easy to recognize isolated pieces of twig or herbaceous stem and this problem is largely overcome by giving attention to large pure stands of a single plant. *Epilobium*, *Urtica*, *Heracleum*, *Filipendula*, *Carex*, *Phalaris*, *Calluna*, etc., provide many such colonies and amply repay careful search. This will prove unfailingly rewarding at the time and unfailingly provocative later for your bag will contain mostly Helotiaceae, Hyaloscyphaceae and Mollisiaceae but, often, too, some little treasure will outshine all the rest.

Similarly, the detritus of each kind of tree carries its own flora; over-wintered involucres of *Castanea*, cones of *Pinus* and *Larix*, catkins of *Salix*, *Corylus* and *Alnus* all offer prospects of a good haul if searched thoroughly for sufficient time.

Rotten trunks should be carefully searched and easily overlooked minute species will often be found tucked away in crevices; half a dozen such may be taken on one good trunk. Every effort should be made to name the host; many fungi are as selective here as upon herbaceous stems but our information on this is meagre owing to so many earlier collections being described as on 'old wood'.

A quite distinct and fruitful habitat is provided by over-wintered sites of bonfires where patches of ash or charred debris may be coral-pink with the confluent apothecia of *Pyronema*; here too we find abundantly *Anthracobia melaloma* with its submarginal fascicles of hairs looking like a ring of dark dots on the pale cortex, *Aleuria umbrina*, deep purple-blue *Galactinia praetervisa*, *Ascobolus atro-fuscus* with its purple-brown heavily-warted spores, pallid *Trichophaea abundans* and many another good thing. Also I think I should mention the new submerged aquatic habitat recently revealed by Ingold (1954) which has already produced interesting new species of Discomycetes and will surely yield others as it is more thoroughly explored.

Lastly, I refer to animal excreta upon which flourish most of the Ascobolaceae. These may be conveniently studied at home by keeping,

for example, a few suitably matured rabbit pellets upon moist cotton-wool in an open dish. In the course of weeks a succession of as many as six or eight species may appear; mostly they are minute and the host must be carefully examined with a lens to keep track of their arrival.

I have already hinted that the host plant or habitat must be accurately recorded. Apropos of the Agarics Quélet wrote to Bataille 'l'habitat est la moitié de la détermination' and this is as true for the Discomycetes. *Dasyscypha crucifera* is restricted to *Myrica gale*; *Sclerotinia tuberosa* is found only in association with *Anemone* and *Rutstroemia luteo-virescens* occurs only on leaf petioles of *Acer*. In such cases accurate naming of the host is almost the whole determination of the fungus but the case is not always quite as simple for two or more closely related species may, and often do, occur on the same host. On stems of *Epilobium* several Mollisias occur of which *Mollisia minutella* Rehm is restricted to this host and on stems of *Filipendula* we find three Mollisias of which *Mollisia millegrana* finds no other host acceptable. Such examples could be much multiplied, and one is tempted to speculate that every host stem may have one or more Discomycetes peculiar to it while providing an acceptable habitat for others less exacting in their demands. At the other extreme we have species such as *Dasyscypha virginea* and *Phialea cyathoidea* with a tolerance so great that we find them distributed over a wide range of hosts.

Looking back to my early collecting days I now realize how much time was mis-spent working upon meagre collections of poor quality. On wood and on herbaceous stems fine colonies are so readily obtainable that it is, indeed, a pity to waste time upon small scattered growths which, by their very poverty, are likely to be of aberrant form. The larger geophilous species present rather a different problem as they are often solitary or only a few together and must be taken as encountered.

Always, too, we tend to collect too much—more than can be given the exacting study now demanded if our work is to make any useful contribution to knowledge; the days are past when a casual look over sufficed. In our foray lists it really serves little purpose to give every red-disked *Scutellinia* the epithet *scutellata* when the chances are at least even that it is not this species. If our studies are to be thorough half a dozen good collections from a local area will suffice at any one time; naturally, when collecting far from home a different outlook must prevail and work upon dried material envisaged.

Here, perhaps, I may refer to the subject of rarity. While many species are doubtless inherently rare, many so-called rarities are only apparently so because we know insufficient about their habitats. *Sclerotinia hirtella* Boud., hitherto of doubtful status in this country, offers an example. This was found in fair quantity in April 1955 on *Castanea* leaf debris during the Society's spring foray at Tring. In the course of the spring foray of 1956 at Flatford Mill we found ourselves in a *Castanea* wood and I instigated a search for *Sclerotinia hirtella* and it was found in plenty—but only because we then knew that it must be sought beneath several inches of the latest leaf fall. *Mollisia urticicola* was until recently known to have been collected but once—by Phillips in the neighbourhood of Shrewsbury; in fact, it is to be found in June in every nettle-bed in Cheshire and adjoining counties

but, probably, mycologists do not spend June crawling about nettle-beds!

The early summer months should not be neglected for they produce rich crops of Discomycetes and particularly of two kinds, the Sclerotiniaceae and the small inoperculates of herbaceous stems. These latter find just the right moist micro-climate on overwintered stems lying in the shelter of the new growth of the year and are then at their peak condition; later in the year the air of such habitats tends to become too stagnant and mildew besets the stems. For good gatherings of the elegant apothecia of the Sclerotiniaceae sustained attention must be given to the appropriate host plants: *Juncus* for *Sclerotinia curreyana*; *Carex* for *Sclerotinia sulcata*; *Alnus* for *Rutstroemia conformata*, etc.

Examining

Let me now say a little about the examination of our finds—each in its own individual box or tin, I hope, and with a scrap of paper on which were noted the details of its occurrence. There is much to do in a hurry before we can relax into their leisurely microscopic examination one by one; we must capture those evanescent features which once lost on drying cannot be recovered; habit, size, colour and all gross morphological characters should be noted and sketches made. A part of each collection may be kept fresh for some time on moist cotton-wool but watch must be kept for the attacks of moulds. Thoroughly to examine everything in fresh condition is sometimes an unattainable ideal and, in such cases, priority should be given to species with delicate hairs such as the operculate Cheilymenias and the inoperculate Hyaloscyphas whose hairs are very difficult to see well on re-soaked dried material.

A minute fragment of the hymenium squashed under a cover-glass in a drop of water will reveal all the hymenial details and, particularly, whether we have an operculate or inoperculate species. The operculum is only to be seen on empty asci which have ejected their spores but the upper part of a mature spore-containing operculate ascus shows a characteristic asymmetry being somewhat swollen on one side and slightly hollowed on the opposite side which will later carry the hinge of the operculum.

When all measurements have been made a drop of iodine (Melzer's reagent) is drawn under the cover-glass and its effect upon the ascus tip noticed. Among the inoperculates there are families in which the pore develops a distinct blue colour and others in which no reaction is shown; a useful specific exception is shown by *Mollisia ligni* in which no colour develops, whereas other commonly occurring lignicolous Mollisias give the blue reaction clearly. Among the operculates the whole of the ascus tip is blued in members of the Aleuriaceae and in the Humariaceae the orange granules in the tips of the paraphyses are changed to green by the same reagent. Measurements should not be made in iodine solutions as many spores—particularly of the inoperculates—shrink considerably therein.

Already in the water mount any ornamentation of the spores may have been noticed but this should be confirmed by squashing another fragment

of hymenium in lactophenol-cotton blue which quickly stains the ornamentation of mature spores and leaves the epispore uncoloured. It should be remembered that complete reticulation may be only the final stage of development from an initial condition of simple warts and that many warted spores and only a few reticulate ones may be seen in a mount of a species said to have reticulated ornament.

We have already accumulated much information about our species but modern taxonomy demands as exacting a study of the flesh of the fungus as of its hymenium, especially in the case of the inoperculates. Mounting one of these, hymenium downwards, in water and pressing down the cover-slip by degrees ultimately brings into view the exterior surface of the cup and we then commonly see one of three kinds of structure: (*a*) a regular pattern of circular, dark-walled, pale cells—the 'textura globulosa' of Dermateaceae; or (*b*) a regular pattern of rectangular or polygonal, hyaline-walled, pale cells—the 'textura prismatica' of the Hyaloscyphaceae; or (*c*) a surface altogether more opaque in which a pattern may be difficult to discern or may appear as rows of radially aligned hyphae—the 'textura intricata' of the Helotiaceae. A 'textura globulosa' of rather large, pale-walled cells is shown by the Orbiliaceae, but these are so distinct from the Dermateaceae in other features that they cannot be confused with these; their curiously wax-like translucency and yellow to orange colour are readily recognized in the field and, microscopically, the hymenium presents unique features such as the small apically-truncate asci with slender bi- or tri-furcate bases and paraphyses suddenly enlarged to an apical knob. Many of the Sclerotiniaceae also show a cortex of pale-walled 'textura globulosa' but, again, are so different from the Dermateaceae in other features that their individuality is at once clear.

This preliminary survey of cell structure must be followed by the cutting of median sections of the fungus attached to a fragment of host. Such sections may be cut very quickly on a freezing microtome and their preparation is an essential to the study of the Helotiaceae and the Sclerotiniaceae, and is desirable also for other families. Such a section now shows the true nature of 'textura intricata' and reveals a weft of undulating and interweaving hyphae very distinct from the parenchymatous structure of (*a*) and (*b*). A section also shows the host relationship and, in particular, the nature of the stroma in the Sclerotiniaceae. An individual large sclerotium such as we find in *Sclerotinia curreyana* is obvious to the naked eye but only a section will reveal a stroma such as that of *Rutstroemia conformata* within the petioles and midribs of *Alnus* leaves. A black base to an otherwise pale stem is often an indication that a stroma may be present. The flesh structures referred to are clearly seen in a vast number of species but there are others of rarer occurrence and outside the scope of this address.

The study of our specimen in culture may also be undertaken and, by this means, it has already been shown that many of the Fungi Imperfecti have Discomycetes for their perfect stage. A very recent example of this is the success of Hickman *et al.* (1955) in persuading the conidia of the Light Leaf Spot fungus of Brassicae to produce a near-Pyrenopeziza perfect stage.

Naming

Thus far, in our collecting, dissecting, drawing, etc., life has been carefree and delightful but one thing is yet lacking—a name for the object upon which we have lavished so much care and attention. Perhaps I can most usefully conclude this address by referring to some of the literature now available with the aid of which we may attempt to complete our task and I shall first mention books which we may reasonably hope to have on our own library shelves. In our own tongue the general works are few. We have Phillips's *British Discomycetes* (1893) and Vol. IV of Massee's *British Fungus Flora* (1895)—the former a valuable collection of personal observations, the latter more of the nature of a compilation and, accordingly, less reliable. Both are over sixty years old but, for all that, contain many excellent descriptions. Thence we must jump half a century for the appearance of Seaver's *North American Cup Fungi* in two volumes, Operculates (1942) and Inoperculates (1951). I find the former most useful for the running down of an unfamiliar specimen prior to turning over to the critical contemporary studies of Mme Le Gal. The latter volume contains valuable sections based on the work of specialists in certain fields, e.g. Whetzel on the Sclerotiniaceae and Groves on the genus *Dermea*. With these four books in hand many good determinations may be made but, as our critical faculty develops, we find that many of our specimens defy our efforts to match them satisfactorily to any description in these volumes. For additional help we must turn to continental works and in Vol. III of *Rabenhorst's Kryptogamen Flora* we find in Rehm's treatment of the Discomycetes (1887–96) an as yet unsurpassed study of these fungi; even, to-day, sixty years after its appearance, this volume must be to hand. Another remarkable general work appeared in 1934 in Velenovsky's *Monographia Discomycetum Bohemiae* with Latin text following interesting introductory chapters in German; the general arrangement closely follows that of Rehm. Although only turning to mycology in his fiftieth year Velenovsky became one of the most assiduous collectors of all time. His book contains descriptions under about 1000 new species names of Discomycetes; many of these will surely be reduced to synonymy but many will stand, for he collected minute species with a persistence and thoroughness hitherto unequalled. The text is accompanied by plates packed with small figures of most of the species described and I find that these are really much better than the impression they first create. Already in Britain several species have been found which match admirably with species novae of Velenovsky.

Of Émile Boudier I have as yet said nothing because we can scarcely hope to possess his superb Icones and because his *Histoire et Classification des Discomycètes d'Europe* (1907) is non-descriptive and is almost devoid of keys to help us find our way about it—an omission which was repaired by Ramsbottom in Vol. IV of our own *Transactions* (1913). Using Boudier's nomenclature Ramsbottom and Balfour-Browne (1951) have recently compiled a list of British Discomycetes which is of considerable value for the extensive literature references given for each species. Boudier, as is well known, divided all Discomycetes into the Operculates and the

Inoperculates according to the two different modes of dehiscence of the ascus; the former were his first love and his classification of these has survived with only minor changes until to-day. However, so closely do other anatomical and visual features align themselves into two parallel series corresponding with the two modes of dehiscence, that groupings closely in accord with these were already emerging prior to Boudier's enunciation of their importance. His system set the seal to the taxonomic struggles of half a century. Its importance, however, has not been everywhere accepted and as recently as 1934 Velenovsky wrote: 'Übrigens warum sollte man mit einem zweifelhaften Merkmale operieren, wenn man andere, viel bessere und verlässliche Charaktere zur Hand hat.' Nevertheless, I feel that when such extraordinary correspondences occur as the almost complete absence of ornamented spores from inoperculate asci and of septation in spores from operculate asci, this elegant though minute detail must, indeed, have a real significance.

In recent years Mme Le Gal has worked devotedly at the Operculates and her critical studies are ever giving additional polish to Boudier's system. Her *Recherches sur les ornamentations sporales des Discomycètes operculés* (1947)—with its numerous fine drawings of sculptured spores—must be in the hands of every serious collector and her latest volume *Les Discomycètes de Madagascar* (1953)—although of limited value in its application to European material—could well serve as a model for the elegant presentation of taxonomic studies. Mention must be made here of the recent studies by Mme Le Gal (1946)—in amplification of earlier work by Chadefaud—on the dehiscence mechanism of the ascus. These have softened the hitherto sharp division between Operculates and Inoperculates by revealing a mechanism partaking of the characters of each of these. This mechanism—the Suboperculate—has been recognized throughout an otherwise homogeneous family, the Sarcoscyphaceae, which are mainly tropical but are represented in this country by the well-known *Sarcoscypha coccinea.*

A new era for the Inoperculates opened in 1932 with the appearance of Nannfeldt's *Studien über die Morphologie und Systematik der non-lichenisierten Inoperculaten Discomyceten.* Utilizing the contents of von Höhnel's scattered and difficultly accessible papers, developing Starbäck's observations on flesh structures and welding these together with the wealth of his own personal researches, Nannfeldt gives us a broadly conceived and coherent picture of the group. This is in no way a text-book for the easy identification of species; rather does it serve to make us think seriously about where any particular specimen really finds its place in the whole pattern. For me this volume has been and remains an ever present source of inspiration.

Taking up two of Nannfeldt's families, Dennis has recently given us *A Revision of the British Hyaloscyphaceae* (1949) and *A Revision of the British Helotiaceae* (1956); in these volumes many of our native species are keyed out, illustrated and described in detail, and there are copious references to continental material; their appearance is the more welcome because they cover families which are always represented in a day's collections and whose members have, hitherto, been difficult to determine with certainty.

Of the earlier classics and of the great work of Saccardo I have said nothing. As individuals we have little hope of owning them and we can refer to them only under library conditions. They are enumerated in several of the volumes to which I have referred and they form an essential background to which, having survived our years of approach to Discomycetes, we are increasingly forced to turn.

As an addendum to this address I have given a short list of smaller monographic works which I have found of much help. I must not leave with you the impression that it is now possible to give a reliable name to every collection we make. Great progress has been made but many of our gatherings must yet remain unnamed pending the publication of careful studies of many genera. Therein lies the challenge of the Discomycetes.

This afternoon I have tried to answer many of the questions so often put to me. I should like to think that some of you may be persuaded to take a greater interest in the fungi of which I have spoken. The amount of work waiting to be done is beyond belief and there are so few putting their hands to it.

In conclusion may I thank my many professional friends at home and abroad for the ever ready help and kindness I have always received from them, and without which my own interest could scarcely have been sustained.

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STUDIES ON SOIL CHYTRIDS

II. ON *KARLINGIA DUBIA* KARLING

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(With 5 Text-figures)

The saprophytic soil chytrid, *Karlingia dubia* Karling, is re-described, with further details of its morphology. The resting spore was found to be formed following a sexual fusion of zoospores, and not asexually as described by Karling.

In this work the chitinophilic chytrid, *Karlingia dubia* Karling, was isolated initially from soil which had been dried and kept in the laboratory for 3 months. Subsequently it was obtained from freshly collected soil from the same site, in Osterley Park, Middlesex, England. The soil was plated-out and baited as described by Willoughby (1956). On this occasion the bait used was shrimp chitin, which was purified by treatment with hydrochloric acid and potassium hydroxide (Karling, 1945). Final refluxing in ethyl alcohol, as recommended by Karling, did not apparently confer any advantage, and this treatment was omitted, although the material was stored in ethyl alcohol at this stage. The bait was boiled and then autoclaved in water prior to use.

Pieces of the chitin bait with mature sporangia on them were removed from the Petri dishes of soil and washed with sterile charcoal water. The chitin was then placed on a slide with a small amount of fresh charcoal water, and warming with an electric lamp induced sporangial dehiscence. The charcoal water containing the zoospores was then looped off into watch-glasses containing fresh sterilized chitin bait immersed in sterile soil-extract solution. In this way a unifungal culture was readily established, and was subcultured by cutting out small portions of the infected chitin and transferring to further watch-glasses with fresh bait and soil-extract solution. Growth under these conditions was extremely rapid at 20° C., and subculturing was necessary at the end of every week, as by this time the chitin was completely covered in thalli. No attempt was made to control or remove bacterial contaminants, which were always present to some extent.

The unique nature of the operculum, the character of the zoospores, the shape and structure of the mature resting spores, and their small size as compared with the sporangia, all agreed well with Karling's (1949*a*) account of *K. dubia*, which was grown on chitin bait: there seems little doubt that the chytrid I have studied should be referred to this species. Karling, however, described the sporangia as developing by general enlargement of the zoospore cyst, while I have found that other types of

development are also possible: further he reported that the resting spores were asexually formed, while the evidence from my material is that they are formed following a sexual fusion of zoospores, which thus appear to be facultative gametes.

The zoospores (Fig. 1) have a posterior flagellum 28–33μ long and are normally spherical, 5·4–6·6μ in diameter. However, any one sporangium can also release elongated zoospores 8–9 by 4μ, and this type has been noticed most particularly in emptying sporangia when the zoospores are motile just before their liberation (Fig. 3 J). Karling states that when the spherical zoospores are trapped in a narrow space they become

Fig. 1. *Karlingia dubia*. Zoospores. Shading has been added to emphasize the position of the vacuole, where this was observed.

elongated; but in my experience elongated zoospores retain this form when they have freedom of motility. However, the elongated form has never been seen in encysted zoospores. Besides the spherical oil drop, which is 1·2–1·6μ in diameter and situated near the insertion of the flagellum, a vacuole can sometimes be seen in the spore. Refractive material may be deposited round part of the vacuole to give a crescent which has no constant orientation to the flagellum, or the vacuole may be completely ringed with refractive material. In encysted zoospores, however, the only refractive region which can be distinguished is the spherical oil drop.

The most usual pattern for sporangial development is that the encysted zoospore develops a single rhizoidal axis, and even enlargement of the cyst outline occurs as growth proceeds (Fig. 2 A–E). This general enlargement usually continues so as to give a sporangium with a perfectly smooth outline as described by Karling (Fig. 3 B, H, J, L); however, growth of the wall may lag behind in one region (Fig. 2 G), which becomes thickened (Figs. 2 H, N, Q–U; 3 D, M). In *Rhizidium elongatum* (Karling, 1949*b*), similar uneven growth of the sporangium occurs, while in *Chytriomyces appendiculatus* (Karling, 1947), a thickened appendage results from the same process. A small proportion of sporangia shows a protuberance which corresponds in size to part of the original zoospore cyst outline, and this may either be unthickened (Fig. 3 K), or thickened (Fig. 3 A). Although the thalli represented by Figs. 2 K and 4 L are possibly stages of development leading to sporangia of this type, it will later be shown that these could, in fact, be young sexually formed resting spores. As further observations were not carried out on these particular thalli, the true position cannot be stated with certainty. In certain cases, part of the

Fig. 2. *Karlingia dubia.* Sporangial development. A, encysted zoospore with first rhizoidal axis developed; B, the same after 2 hr. further development; C–F, young thalli; G–K, young thalli showing uneven growth (a thickened region of the sporangium wall has developed in some cases); L, M, young thalli showing an unusual rhizoidal development which is sometimes encountered; N, young thallus showing separate rhizoidal insertions; O, P, young thalli with part of the thickened zoospore cyst as a cap to the thickened region of the sporangium wall; Q, part of a dehisced sporangium showing thickened region of the sporangium wall; R–T, thickened region of wall in developing sporangia; U, part of a mature sporangium showing thickened region of the wall. All drawings at same scale except L and M.

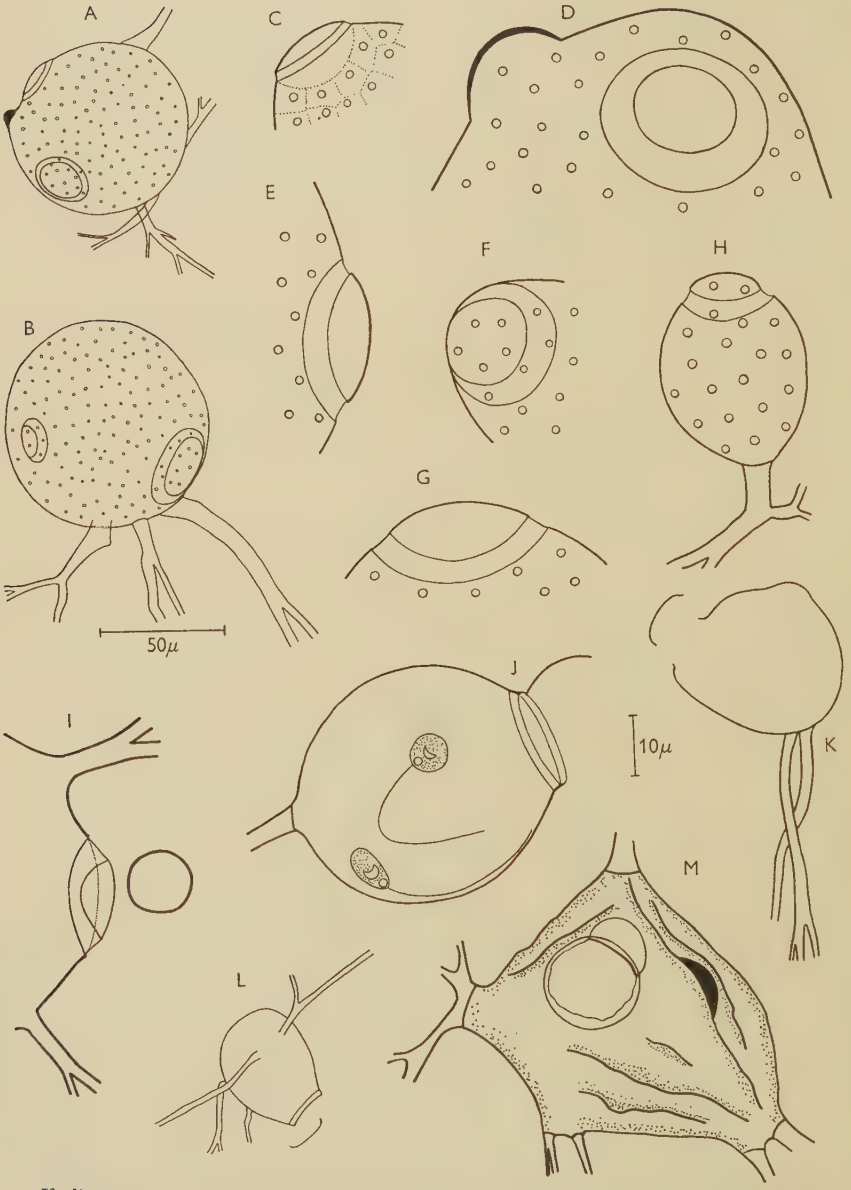

Fig. 3. *Karlingia dubia*. Mature and dehisced sporangia. A, mature sporangium with thickened zoospore cyst; B, mature sporangium with two opercula; C, operculum with clear zone of cytoplasm below it (the cytoplasm is drawn in optical section and the operculum in surface view); D, part of a mature sporangium showing operculum and thickened region of the wall; E–G, opercular regions of mature sporangia; H, mature sporangium; I–M, dehisced sporangia. In the sporangia illustrated in J and K respectively, the former has two zoospores remaining, one showing the elongated form, and the latter has part of the original zoospore cyst wall persisting unaltered as a projection from the sporangium wall. A, B, L, at scale shown below B. Others at scale shown above M.

thickened zoospore cyst occurs as a cap to the thickened region of the sporangium wall (Fig. 2O, P).

At maturity the sporangia are oval and $20 \times 18\mu$ to $230 \times 136\mu$, or spherical and $17–144\mu$ in diameter. They have one to four opercula, and usually a number of rhizoidal axes inserted separately on the sporangium. When the opercular region is examined in side view with a 1·8 mm. objective, two distinct rims can be seen in an upper focus (Fig. 3A–H). The appearance suggests that splitting of the outer wall of the sporangium has occurred, and that stretching has resulted in the separation of these two rims, with the intercalation of a thinner part of the wall between them. Although a preliminary formation of a thickening ring has not been demonstrated, it is considered that the opercula of *K. dubia* develop in a similar way to the 'caps' of the alga *Oedogonium*. In favourable cases a zone of clear cytoplasm can be seen below the operculum, together with the outlines of the delimited zoospores (Fig. 3C).

The bulk of the zoospores emerge as one mass, rather slowly, and become actively motile after a short time. The remaining zoospores tend to escape individually. In favourable examples it is possible to see that the thin portion of the sporangium wall above the lower rim of the opercular region remains in position when the operculum separates (Fig. 3I). Karling's suggestion that this thin portion of the sporangium wall may be part of the wall of an endosporangium has not been supported by my observations.

As a preliminary to sexual fusion, the gametes, which become distinguishable from other zoospores only by their greatly reduced motility, can often be seen in groups in close contact with each other. Pairs of gametes, apparently entangled by their flagella, have frequently been seen moving jerkily together. They come to rest on the substratum in contact with each other, and by this time are encysted. A rhizoidal system develops from one of them, but there is no increase in size of either cyst. Some time elapses before there is any outward sign of fusion, and then a narrow connecting bridge can be seen. The widening of this bridge to give a roughly oval structure then proceeds rapidly, and this has been followed by using a 1·8 mm. objective on a normal mount of the material in soil-extract solution (Fig. 4A–D). The preparation was frequently irrigated, and saturated cotton-wool placed at the cover-glass edge to prevent drying-up. The outlines of the original zoospore cysts are still recognizable as the rounded ends of the developing resting spore at this stage, but these are usually lost as further development takes place. This further development normally involves a size increase in all directions, until at maturity the resting spore is spherical or nearly so, $12–25\mu$ in diameter, and has brown thickening material up to 2μ wide deposited inside the original wall, which is still distinguishable. At maturity the cytoplasmic contents are apparently contracted away from the wall and a central vacuole is also visible (Fig. 4P, R). Complete development of the resting spore from the pair of gametes takes approximately 3 days, and this has been followed using a hanging-drop technique (Fig. 5A–F). In some of the resting spores, and especially the smaller ones, a small hemispherical projection is seen, and this represents part of the outline of the original zoospore cyst most remote

from the initial rhizoidal axis (Fig. 4O, S, T). This hemispherical projection is usually thickened in the same way as the rest of the resting spore wall. Karling, in his account of *K. dubia*, illustrates a similar projection on two resting spores, but does not mention how it could have been formed.

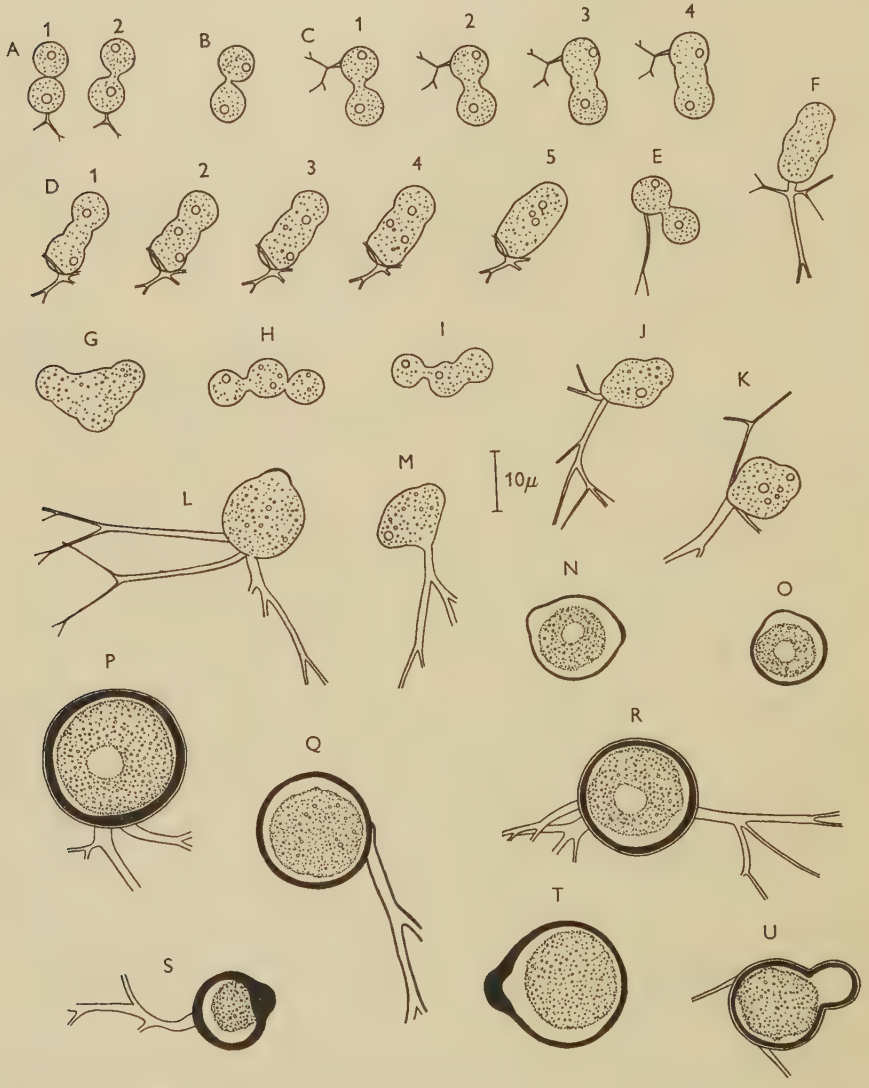

Fig. 4. *Karlingia dubia*. Resting spore formation. A, 1, 2, successive stages in fusion of gametes; B, pair of gametes with connecting bridge; C, 1–4, and D, 1–5, successive stages in fusion of gametes; E, F, stages in fusion of gametes; G–I, triple fusions of gametes; J, K, developing resting spores; L, developing resting spore or sporangium; M, developing resting spore showing unusual position of the initial rhizoidal axis, which is inserted at the connecting bridge; N, mature resting spore showing two hemispherical projections; O–T, mature resting spores; U, mature resting spore of unusual kind with an adherent thick-walled empty cyst of greater dimensions than the normal zoospore cyst.

Some small resting spores show two such hemispherical projections, representing parts of the outlines of both of the original zoospore cysts, and in these cases wall thickening is not very great. There is, however, the normal apparent cytoplasmic contraction from the wall, and the central vacuole (Fig. 4N).

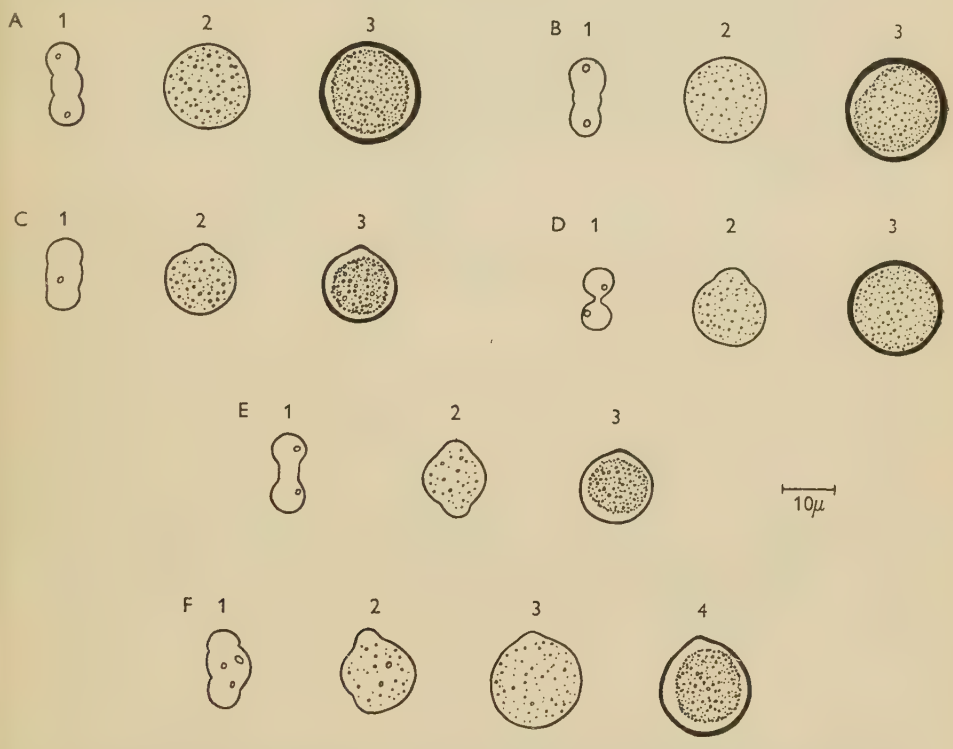

Fig. 5. *Karlingia dubia.* Resting spore formation. A–F each shows successive numbered stages leading to resting spore formation, as observed under hanging-drops. Rhizoidal systems have been omitted.

There is evidence that triple fusions of gametes occur on occasions (Fig. 4G–I). Presumably resting spores result, although it has not been possible to verify this.

It is seen that in *K. dubia* there is no residual empty cyst resulting from sexual fusion, as there is in the genus *Rhizophidium*, although in a single instance (Fig. 4U), a structure was found which could almost be interpreted as such. There is normally a loss of identity of the two cysts following fusion, and both become incorporated in the resting spore. Sparrow (1943) evidently attached special significance to this loss of identity of two cysts following fusion, which phenomenon he regarded as representing a primitive type of sexuality in the Chytridiales. While conceding that this state of affairs occurs in the Olpidiaceae and Synchytriaceae, both of which have a holocarpic organization, he regarded the records of Sorokin in 1874 and Gimesi in 1924 for eucarpic chytrids as not fully authenticated.

However, Hanson (1944) has more recently described a eucarpic chytrid with a sexuality of this type; where the resting spore is formed following a fusion of two equal gametes, one of which has previously come to rest and germinated. Furthermore, the developing resting spore of this chytrid is similar to that of *Karlingia dubia* in that the apex is often lobed, and these lobes represent the vestiges of the original gametes.

It is apparent that the differences between the Chytridiales and the Blastocladiales are becoming increasingly indistinct (Karling, 1951); it is hardly surprising that a sexual fusion very similar to that commonly found in the latter order should also occur in the Chytridiales. Members of the Blastocladiales show greater morphological complexity than is found in the Chytridiales, and there is no reason for supposing that this type of sexual fusion is restricted to those chytrids which are least developed morphologically and which from this view point might be considered as most primitive. It seems that greater knowledge is required before any theories regarding the phylogeny of members of the Chytridiales can usefully be put forward.

In the meantime the present account represents the first record of a sexual process in *Karlingia*, a well-established genus of the soil chytrids, and members of which have been reported from America and Europe. Further British representatives of the genus which are being studied will be discussed in due course.

My thanks are due to Professor C. T. Ingold for his help and advice with this investigation. The work has been carried out with the aid of a maintenance grant from the Department of Scientific and Industrial Research, to whom acknowledgement is made.

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THE GENUS *PAECILOMYCES* BAINIER AND ITS PERFECT STAGE *BYSSOCHLAMYS* WESTLING

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(With Plates 1 and 2, and 16 Text-figures)

CONTENTS

PAGE

Historical introduction
Paecilomyces 17
Byssochlamys 19
Occurrence and economic importance 24
Biochemistry 27
Materials and methods 28

Taxonomy

Paecilomyces—generic diagnosis; the colony; sporing structures 30
Byssochlamys—generic diagnosis; the colony; ascospore formation; ascospores . 32
Key to species of *Byssochlamys* and *Paecilomyces* 33
Descriptions of species of *Byssochlamys* and *Paecilomyces* which have been studied in culture 35
Descriptions of species of *Paecilomyces* which have not been examined in culture, and which are accepted only provisionally 73
Some fungi, mostly described as species of *Spicaria*, but which are probably to be excluded from *Paecilomyces* 76
References 83
Explanation of plates 88
Index 88

HISTORICAL INTRODUCTION

Paecilomyces

The form-genus *Paecilomyces* was erected by Bainier (1907) on the single species *P. varioti*. Bainier emphasized its relationship to *Aspergillus* and *Penicillium* and gave as its distinguishing features: colonies fulvous, with only a suggestion of a green tone; fruiting structures very diverse (hence the name from ποικιλος = varied), consisting of single sterigmata (i.e. phialides) scattered along the aerial hyphae, or of small clusters of sterigmata, or fairly complex penicillate systems, often with one whorl after another, of branches and sterigmata, along the length of the conidiophore. What is regarded at the present day as one of the most important characters, the shape of the phialides, is not mentioned by Bainier but is well brought out in his figures.

Bainier's paper attracted little attention at the time. His figure was

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listed in *Index Iconium* (Saccardo, *Sylloge*, **20**, 1911), and in *Sylloge*, **22**, 1913, *P. varioti* was transferred to *Penicillium*.

The next mention of the mould was by Thom (1910) who, unaware of Bainier's paper, described it independently as *Pen. divaricatum*. Thom's paper was widely studied, since it was the first time that some sort of order had been brought into the genus *Penicillium*. His description of the mould was detailed and accompanied by carefully drawn figures, and most references to *P. varioti* during the next two decades are to be found under the name *Pen. divaricatum*.

Westling (1911), in his monograph on *Penicillium*, discusses the question of species which are not green. He refers to Thom's *Pen. divaricatum* and *Pen. lilacinum*, stating that they do not belong in *Penicillium* but must be transferred to other genera. Although he goes out of his way to call the reader's attention to Bainier's paper on *Scopulariopsis*, he does not seem to have known of *Paecilomyces*, published in the same journal and in the same year.

Sopp (1912) described a new genus *Corollium*, to include a fulvous mould which he found on army boots in store. From his description and figures there is little doubt that his *C. dermatophagum* is another synonym of *P. varioti*. Sopp, like Thom and Westling, seems to have been unaware of Bainier's description of *Paecilomyces*.

Biourge (1923) examined a culture said to be *Pen. divaricatum*, obtained from Kral, and reported that it was a *Scopulariopsis*. However, he stated, probably with reason, that the Kral culture was suspect, and his figures certainly indicate that he had a *Scopulariopsis* and not *P. varioti*. It is just possible that he had one or more isolates of *Paecilomyces* in his collection for, in discussing his group 'Anomala', he says, 'Plusieurs représentants du group ont leur *phialides terminées en longues soies*' (the italics are Biourge's), but, except in his bibliography, he does not mention Bainier's genus.

Zaleski (1927) was apparently unacquainted with both *Scopulariopsis* and *Paecilomyces*, either under these or any other names. In classifying his Penicillia he followed the scheme of Biourge and, after describing the species in several subsections, he says 'Für die übrigen Untersektionen (IV Stellata, V Fragilia, VI Anomala, VII Polyverticillata) habe ich keine Art gefunden'. Nowhere in his monograph is there any suggestion that any of the species are other than true Penicillia.

Thom (1930) recognized Bainier's genus *Paecilomyces* and devoted a chapter to it. He stated that *Pen. divaricatum* is to be regarded as a synonym of *P. varioti*, and listed as being in all probability congeneric: *Corollium dermatophagum* Sopp, *Spicaria fimetaria* Moesz, *Pen. repandum* Bainier et Sartory, *Pen. burci* Pollacci, *P. varioti* Bainier, *Pen. flavum* Él. et Em. Marchal, *Pen. aureo-cinnamomeum* Biourge, *Eidamia catenulata* Horne et Williamson, *Byssochlamys nivea* from Pribram, *Pen. mandschuricum* Saito, *Pen. arenarium* Shaposhn. et Mant., together with isolates without names from Hansford, Kita, Pribram and Turesson. Thom described the genus in more precise terms than Bainier's and made the following new combinations: *P. aureo-cinnamomeum*, *P. burci*, *P. mandschuricum*. *P. varioti* was described in such terms as made it easy for anyone to recognize the species, with the result that most records of its occurrence subsequent to 1930 have been under the correct name.

Kennelly & Grimes (1930) described what they believed to be a new species, *P. hibernicus*.

Raper & Thom (1949) continued the use of the name *Paecilomyces*, but contributed little to our knowledge of the genus.

Hughes (1951) redescribed *Pen. elegans* Corda from fresh collections and transferred it to *Paecilomyces*. He also made the new combination *P. marquandii* (= *Verticillium marquandii* Massee).

In the meantime Abbott (1926*a*) described a new species of *Spicaria*, *S. violacea*, and this was again described in a paper on soil fungi by Gilman & Abbott (1927). Gilman (1945) regarded *P. varioti* as congeneric with *S. violacea* and transferred it to *Spicaria*. Raper & Thom (1949), whilst provisionally recognizing *S. violacea* as related to, but distinct from, *Pen. lilacinum* Thom, did not suggest placing *P. varioti* in the same genus.

Byssochlamys

The genus *Byssochlamys* was erected by Westling (1909) on the single species *B. nivea*, isolated from a *Geaster* which had been preserved in spirit. The fungus was characterized by the production of 8-spored asci in irregular clusters without any suggestion of a peridium; of phialospores, the phialides being sessile on aerial hyphae or borne on more or less penicillate branching systems; and of small chlamydospores. Further it was found to be extremely resistant to alcohol. It was suggested that the new genus forms a link between the Endomycetaceae, with solitary 4-spored asci, and the Gymnoascaceae, with numerous 8-spored asci surrounded by a loose web of hyphae.

Westling's record of the species remained the only one until J. H. Warcup isolated what is undoubtedly the same species from soil at Clophill, Beds, and kindly supplied a culture for the present study.

Olliver & Smith (1933) described a second species, *B. fulva*. This was creating a nuisance in the fruit canning industry, since the ascospores are able to withstand a temperature of 86–88° C. for 30 min. in fruit syrup, and some spores frequently survive a processing temperature of 90° C. It is distinguished from *B. nivea* by its fulvous colour, abundant production of conidial structures of the *P. varioti* type, and the somewhat larger size of the ascospores.

A third species was described by Naumoff & Kiryalova (1935) and, since it was isolated from must of grapes, was named *B. musticola* (stat. conid. *Spicaria musticola*). It is impossible to tell with certainty, from the meagre descriptions, whether this is a good species, but, if it is a *Byssochlamys*, then the description 'conidiis hyalinis dein dilute-ochraceis' suggests that it is close to, if not identical with, *B. fulva*.

The status of the genus Paecilomyces

There is no doubt that *Paecilomyces* is closely related to *Penicillium*. At the same time no one who knows the latter genus at all well has any doubt that *Paecilomyces*, at least as represented by the type and most common species, is sufficiently distinct from the majority of the Penicillia to justify Bainier's creation of the new genus. The rediscovery of the perfect state, in

B. fulva, and the fact that the conidial state of the latter is almost indistinguishable from *P. varioti*, raises anew the question of the status of the form genus.

In *Penicillium* there are two distinct types of ascocarp. In the *Carpenteles* series and the *Pen. javanicum* series the perithecia develop as sclerotium-like bodies, in which the asci gradually develop from the centre outwards. In the *Pen. luteum* series the ascocarp may have a definite peridium, as in *Pen. stipitatum*, or may be enclosed by a soft web of interwoven hyphae, as in *Pen. luteum*, but in all cases it is of comparatively rapid development, is usually brightly coloured, and is of limited and fairly definite size. In *Byssochlamys* the ascogonium is very similar to those of *Pen. luteum* and *Pen. bacillosporum*, but the ascocarp (if it can be so-called) is of indefinite size and consists of an irregular cluster of asci without the least suggestion of peridium. If this were the only difference between *Byssochlamys* and *Pen. luteum* it might be justifiable to regard the two as congeneric, but, when the differences in morphology of the imperfect fruiting structures are taken into consideration, we are of the opinion that there is sufficient reason for regarding *Paecilomyces* as distinct from *Penicillium*. Nevertheless, quite apart from any similarities between the respective perfect states, the two genera converge at various points. *P. marquandii* and *Pen. lilacinum* show many similarities even when typical specimens are compared, and, in addition, many intergrading forms are known. Other species which are here regarded as *Paecilomyces* approach *Penicillium* in other single features—shape of spores, shape of phialides, or colour of colonies—but in each of the species the sum total of characteristics is sufficient to place them indubitably in *Paecilomyces* rather than in *Penicillium*.

A few species of the genus tend to approach *Gliocladium*, in that the conidia are not completely dry and, in a moist atmosphere, tend to slime down into irregular masses. Some species which show this tendency and which, in addition, produce a preponderance of solitary phialides instead of penicillate fruiting structures, provide a link with *Cephalosporium* and *Verticillium*.

Other genera in which species of Paecilomyces *have been placed*

Coremium Link. A. L. Smith (1919) described a fungus on a wasp as *Coremium swantonii* n.sp. Petch (1931, 1936) stated that *C. swantonii* is a synonym of *Isaria farinosa*, which in 1934 he had transferred to *Spicaria*. *I. farinosa*, as usually interpreted, is undoubtedly a *Paecilomyces* (see p. 50). However, the original description of *C. swantonii* is too inadequate to hazard more than a guess at its identity.

Corethropsis Corda. Vuillemin (1930) described a fungus from a human mycosis as *Corethropsis puntonii* n.sp. Nannizzi (1934) transferred this species to *Paecilomyces* and Baldacci (1938) made an extensive study of the fungus and its pathogenicity, and states that he fully agrees with Nannizzi's transference. A culture from CBS, Baarn, labelled *P. puntonii*, corresponds with the original description and is a good *Paecilomyces*.

Corollium Sopp. Thom suggested in 1930, and Raper & Thom (1949) agree, that *Corollium* is a synonym of *Paecilomyces*.

C. dermatophagum occurred on tanned leather, forming a growth which was bright brown to somewhat greenish yellow, thick and velvety. It was found to be thermophilic. Sopp's extensive descriptions (1912) are unfortunately deficient in the details which are now regarded as of the greatest importance by students of *Penicillium* and related genera. Hence, since Sopp did not distribute cultures, there is bound to be some conjecture when trying to determine what his material represented. However, there is little doubt that his *C. dermatophagum* is a synonym of *P. varioti.*

Eidamia Lindau. Horne & Williamson (1923) described what they regarded as two new species of *Eidamia. E. catenulata* was rightly determined by Thom (1930) as *P. varioti.* Its inclusion in *Eidamia* was based on its production of terminus spores, now usually termed 'macrospores', in addition to catenulate conidia. The other 'new species', *E. viridescens*, is undoubtedly *Trichoderma viride* Pers. ex Fr., which, apart from its production of somewhat similar macrospores, shows nothing which would justify its inclusion in the same genus as *E. catenulata.*

Hormodendrum Bonorden. The genus was erected in 1851 on four species which had been described by Corda as species of *Penicillium.* The type, *H. olivaceum* (Cda.) Bon. is probably a *Cladosporium* and is certainly not congeneric with the other three species. Of these, *Pen. elegans* Corda has been shown by Hughes (1951) to be a *Paecilomyces.*

Isaria Pers. ex Fr. It is not unusual for some species of *Paecilomyces*, particularly when growing on natural substrata, to form erect fascicles and even definite coremia. These species have often been referred to the genus *Isaria.*

I. farinosa, a common parasite of insects, has been well known since it was described by Dickson in 1790, but it was not until Vuillemin (1911) described the method of conidium production that its real systematic position became clear. Petch (1934), in a paper on *Isaria*, discussed methods of spore production and pointed out, as Vuillemin had already done, the heterogeneous nature of the genus. He suggested that, if *I. farinosa* Pers. ex Fr. be the type species of the genus *Isaria*, then the latter is merely a coremial form of *Spicaria.* However, Petch did not consistently abandon *Isaria*, but described coremial *Spicaria*-like fungi thus: *Spicaria* (*Isaria*) *dubia* (1937), *S.* (*I.*) *laxa* (1937), *S.* (*I.*) *fumoso-rosea* (Wize) Vassil. (1944). The systematic status of the genus *Spicaria* is discussed below.

It should be noted that species of *Paecilomyces* which normally produce isarioid growths on insects and other natural substrata seldom produce coremia in artificial culture.

Mariannaea Arnaud. Arnaud (1952) based the monotypic *Mariannaea* on *M. elegans*, stating that it resembles *Clonostachys* Corda except that the chains of conidia are divergent instead of being packed together. He also states that his species shows affinities with *Spicaria elegans* Corda (*sic*). The figures clearly indicate a *Paecilomyces*, and, from the description, and habitat, it is almost certain that *M. elegans* is to be regarded as a synonym of *P. elegans* (Corda) Mason et Hughes.

Penicillium Link. Corda described four new species of *Penicillium*, *Pen. verticillatum* (1837), *Pen. elegans* and *Pen. anomalum* (1838), and *Pen. olivaceum* (1839). These are certainly not congeneric. *Pen. olivaceum* is almost

certainly a species of *Cladosporium*; *Pen. anomalum* and *Pen. verticillatum* are probably undeterminable, although Biourge (1923) considers the former to be a *Scopulariopsis*; whilst *Pen. elegans* has been redescribed by Hughes (1951) as *P. elegans*.

Pen. divaricatum Thom (1910) is a synonym of *P. varioti* (see p. 18). The relationship of *Pen. lilacinum* Thom to *P. marquandii* (syn. *Spicaria violacea* Abbott) is discussed on p. 64.

Spicaria Harting. Many species of *Paecilomyces* have been described under *Spicaria*, the latter name having been used frequently for white or pale-coloured moulds with more or less penicillate conidial fructifications. However, there is good reason for regarding the name *Spicaria* as a *nomen ambiguum*, whereas there is no confusion whatever regarding the type species of *Paecilomyces*.

The genus *Spicaria* was erected by Harting in 1846 on the single species *S. solani*, which formed pustules on potato. He gave a fairly full description of his fungus and some drawings (Pl. 1, figs. 1, 2). He regarded it as similar to *Verticillium* Nees, but without lateral branches.

The genus was resurrected by Harz (1871) with an emended diagnosis and one new species, *S. nivea*. His description and figure suggest that the latter is a species of *Paecilomyces* (Pl. 1, fig. 3). He points out that the characteristic of the genus is the several times verticillate branching of the conidiophore, and, in his diagnosis, he describes the conidium-bearing cells as cylindrical or most often narrowing towards the tip and slightly thickened at the very end. This is very suggestive of a tapering phialide with a young conidium still attached to the narrow tip. It is true that he describes and figures conidia occurring in branched chains, but it is highly probable that this is a case of his having seen one chain lying partly on top of another or crossing it, and that his conidium-bearing branches are truly phialides.

Harz also transferred to *Spicaria* three of the species which Corda had placed in *Penicillium* and Bonorden in *Hormodendrum*. He apparently made the transfers without seeing any exsiccata and entirely on the descriptions and figures in Corda's *Icones*. In so far as *Spicaria sensu* Harz is a synonym of *Paecilomyces* he was right in his transfer of *Pen. elegans*, but on less sure ground with *Pen. verticillatum* and *Pen. anomalum*.

Harz's interpretation of *Spicaria* soon gained general acceptance. Saccordo (*Sylloge*, **4**, 167) cites *Spicaria* Harz and he obviously accepts Harz's interpretation of the genus. Under *S. nivea* he states: '*Spicaria solani* is different from the above and is, according to Franks, *Acrostalagmus cinnabarinus*. On the contrary *Spicaria Solani* Riv. Parass., p. 563, fig. 304 (conidia solitary, ovoid, 5–8 × 4 μ) is a *Verticillium* species, e.g. *V. candidulum* var. *Solani*.' The latter is cited again in *Sylloge*, **22**, 1298, as *V. candidulum* var. *solani* (Riv.) Sacc., with *S. solani* Riv. as synonym. According to Petch (1945) it is possible that this is identical with the conidial stage of *Nectria solani* Reinke et Berth. However Petch, recording *N. solani* on potato in Britain, says: 'On these specimens there also occurred minute white tufts of conidiophores, scattered or gregarious. These are the conidial stage figured by Reinke and Berthold, who referred it to *Spicaria solani* de Bary.' After describing the fungus Petch continues: 'This is a *Gliocladium*, which

must stand as *Gliocladium solani* (Harting) Petch. Reinke and Berthold employed the name *Spicaria solani* de Bary, Die gegenwärtig herschende Kartoffelkrankheit, etc. (1861), p. 43. But de Bary took the name from Harting (1848) [*sic.*], as also did Schacht (1856)....De Bary's description and figure indicate a *Gliocladium*.' Schacht's figure indicates a *Paecilomyces*, certainly not a *Gliocladium*, and is evidently neither Harting's species nor Petch's. Harting's figures, as indicated below, do not fit in either genus. In any case Harting did not suggest any connexion between his *Spicaria* and an Ascomycete, nor did Petch produce any evidence that his *Gliocladium* was not an entirely separate fungus from *N. solani*.

In addition to Saccardo, Vuillemin (1911, 1912), Fron (1911), Petch (many refs.), Gilman & Abbott (1927), Abbott (1926*a*, *b*), Gilman (1945), and many other authors followed Harz. Gilman & Abbott went so far as to describe *P. varioti* as *Spicaria divaricata*. Raper & Thom (1949) accepted *S. violacea* Gilman et Abbott, but, although Gilman & Abbott had already described this as congeneric with *S. divaricata*, they nowhere suggest that *S. violacea* should be placed in *Paecilomyces*.

Apparently the first to query the current interpretation was Owen (1919), in a paper on the skin-spot disease of potato tubers. After quoting Harting's description of *Spicaria* she says: 'It is clear from the above, and especially from the figures, that the genus *Spicaria*, as founded by Harting on *S. solani*, does not correspond with the generally accepted views of the genus, which, according to Saccardo (*Sylloge*, **4**, p. 167) are rightly interpreted by Harz (*Bull. Imp. Natur. Moscow*, **44**, 1, p. 167, 1871). *S. solani*, as described by Harting, would appear to belong not to the Mucedineae, as commonly supposed, but to the Tuberculariеae. The figures suggest that *S. solani* is closely related to the genus *Tubercularia*, if indeed it should not be referred to it.' Owen's clear exposition has received little attention until very recently, and Harz's mis-interpretation has continued to be widely accepted.

Hughes (1951) transferred *Verticillium marquandii* Massee to *Paecilomyces*. In the present investigation *P. marquandii* has been found to be identical with *S. violacea*, and as Massee's name has priority the epithet *violacea* is a synonym. Hughes also published a careful description of *Pen. elegans*, based on a number of fresh collections and cultures which had been checked by comparison with Corda's exsiccata. He says: '*Spicaria* Harting, in which genus the fungus was classified by Harz, is confused (see Owen, 1919) and from the diagnosis it is impossible to gather much of its systematic position. The type species, *S. solani* Harting, does not seem to have been redescribed, so it is best for the time being, therefore, not to use the name.' He follows this by making the new combination *Paecilomyces elegans*. We are in full agreement with Hughes's remarks, and consider with him that the name *Spicaria* is best forgotten.

Petch described many new species of *Spicaria* in his 'Studies on entomogenous fungi'. In most cases his diagnoses are all too abbreviated and lacking in essential data, and are seldom accompanied by figures. So far as can be ascertained he never defined his own conception of the genus *Spicaria*, so it must be supposed that he adopted the interpretation which was current, that of Harz popularized by Saccardo. His exsiccata at the

British Museum (Nat. Hist.) have been examined and those specimens in which any recognizable structures remain show typical *Paecilomyces*-like fructifications.

Verticillium Nees ex Wallr. *V. marquandii* Massee (1898) has been redescribed by Hughes (1951) as *P. marquandii* (see p. 62).

Occurrence and economic importance

Species of *Paecilomyces* and *Byssochlamys*, referred to as such or as species of *Spicaria* or *Penicillium*, have been reported as occurring on a wide range of substrata and from all over the world. Their chief economic importance is as causes of damage to all kinds of organic materials. A few species have been reported as mildly pathogenic to humans. Others, almost without exception referred to *Spicaria* in the literature, are parasitic on insects and sometimes cause epidemics amongst them. No case of any species being pathogenic to a plant has been described.

Foodstuffs

Fruit. Canned and bottled fruits are damaged by *Byssochlamys fulva*, which destroys the pectin and causes the fruit to disintegrate (Olliver & Smith, 1933; Olliver & Rendle, 1934; Gillespy, 1938, 1941; Hull, 1939). The fungus is found in soil and on decaying fruit in orchards, and is carried into the factory with the early soft fruits. The ascospores are very resistant to heat and, unless processing is carried out at a higher temperature than was at one time considered suitable, some spores survive.

Species of *Paecilomyces* have been recorded on market fruits by Marchal & Marchal (1921) as *Pen. flavum*; Moll (1930) as *Spicaria* sp.; and Lentz (1941) as *Spicaria* sp.

Fermented liquors and fruit juices. Saito (1921) described *Pen. mandschuricum* (=*P. varioti*) as occurring in sorghum brandy. Sakaguchi, Inoue & Tada (1939) isolated their *Pen. viniferum* (=*P. varioti*) from grape juice. Naumov & Kiryalova (1935) described *Byssochlamys musticola* from must of grapes.

Butter. Bisby, Jamieson & Timonin (1933) found *Pen. divaricatum* (=*P. varioti*) to be common in Manitoba butter. Kennelly & Grimes (1930) described, as a new species, *P. hibernicus* (=*P. fumoso-roseus*) from Irish butter. Macy, Combs & Morrison (1931) reported *Spicaria* sp. amongst the fungi found in a churn.

Miscellaneous foods. Raper & Thom (1949) record *Paecilomyces* sp. from licorice root, hens' eggs, nut margarine, soya products in China, bread in Arabia, and in quinine solution.

Wood

P. varioti causes a yellow staining of oak wood, a condition called by Williamson (1923) 'golden oak', to distinguish it from 'brown oak'. Since 1923 the action of *P. varioti* (usually referred to as *Pen. divaricatum*) on oak has been studied by Hubert (1929), Davidson (1935), Cartwright & Findlay (1936), and Cartwright (1937). It was found in the heart wood of living oaks by Davidson, Campbell & Vaughn (1942), and was reported

by Robertson (1939) to stain oak wood during kiln drying. Fisher (1940) found that timber attacked by *P. varioti* is more susceptible than sound wood to infestation by the death-watch beetle. Rennerfelt (1937) includes *P. varioti* amongst the fungi which cause discoloration of ground wood pulp.

It is interesting in this connexion that *Pen. elegans* Corda was found on the inner surface of loose bark of rotting trunks of fir trees.

Paper and textiles

Sée (1919) describes *Spicaria elegans* var. *flava* (= *P. varioti*) from blotting paper. Bakhtin (1928) found *S. elegans* causing deterioration of books in the State Public Library of Leningrad. *P. varioti* was used as a test organism by Lavers & Illman (1946) in an investigation of the increase in water-vapour transmission of packaging materials caused by mould growth. *P. varioti* has been isolated from rotting filter-paper in the L.S.H.T.M. laboratories.

A number of strains of *P. varioti* examined in the present study were isolated from cotton yarns. Partridge & Key (1949) used the same organism for testing yarn for rot proofness. Macmillan & Basu (1947) and Basu (1948) found *P. varioti* as a cause of damage and staining of jute. Smith (1945) recommended *P. varioti* as one of the test organisms for work on tropic proofing, since it was one of the moulds most frequently found on mildewed goods returned from the tropics.

Leather

Sopp (1912) described *Corollium dermatophagum* (= *P. varioti*) as common on army boots and other leather goods in military stores. The growth of *P. varioti* on leather and methods of prevention were discussed by Orthmann & Higby (1929). Hausam & Liebscher (1940) described spotting of tanned sheepskin by *Paecilomyces* and other fungi.

Miscellaneous

Species of the genus are commonly isolated from soil and several species have been described as growing on rotting vegetation. Bainier's (1907) *P. varioti* had been isolated by Variot from decomposing osiers; Saccardo (1886) isolated *S. griseola* from rotting leaves; Ellis & Everhart (1883) isolated *S. fumosa* from the spines of old chestnut burrs; and von Szilvinyi (1936) obtained *Pen.* (*P.*) *victoriae* from tobacco in Sumatra.

Smith (1945) mentioned *P. varioti* as 'the only mould found, so far, on phenolic plastics'. Thom isolated his type strain of *Pen. divaricatum* from a pot of library paste. Thom & Raper (1932) obtained a *Paecilomyces* from sandy loam containing enough arsenic to prevent growth of various crops; when grown on arsenic-containing media it rapidly liberated gaseous compounds of arsenic. Sakaguchi *et. al.* (1939) obtained their *Monilia formosa* (= *P. varioti*) from a botanical specimen preserved in dilute formalin. Westling's *Byssochlamys nivea* was found growing on a *Geaster* which had been preserved in alcohol. Moesz (1921) isolated *Spicaria fimetaria* (*Paecilomyces* sp. indet.) from horse dung. Rettenberg (1940)

in an investigation of the microflora of marine air, found both *Paecilomyces* and *Spicaria* species. Conant, Martin, Smith, Baker & Callaway (1945) record *Paecilomyces* as a common contaminant of plates used for growing dermatophytes.

Insects

The literature on entomogenous species of *Spicaria* is extensive, and we have endeavoured to examine as much as possible of it which is pertinent to this study. Nevertheless, we do not pretend to have made an exhaustive search, since it soon became apparent that the diagnoses of species of *Spicaria* and *Isaria* are, with few exceptions, too scanty to be of much use, and are very rarely based on cultures. Petch (1925–44) described many species of *Spicaria*, most of which should undoubtedly be referred to *Paecilomyces*. Charles (1941) has published a check list of entomogenous fungi of N. America and includes many species of *Spicaria*.

A few species have been observed to attack and sometimes kill beneficial insects, e.g. silkworm (Mascera, 1940). Other species parasitize insects which damage agricultural crops, and, since this phenomenon was first observed, there have been many attempts to make deliberate use of these fungi for the control of noxious insects. Laboratory-scale experiments have sometimes been successful, but attempts to induce epidemics in the field have failed. Petch (1925*c*), who took a great interest in this problem, says: 'No fungus disease has ever exterminated an insect or prevented an epidemic. That such diseases do kill off large numbers of insects periodically, and so exercise a considerable natural control, is undoubted, but it has not yet been possible to improve on nature in this respect. . . but at the present time the available evidence is decidedly opposed to the idea that any practical use can be made of them.' Fawcett (1944), however, maintains that failure to improve on natural control is often due to a 'natural spore saturation', and that where the natural spore density is below saturation infection can often be spread artificially.

Pathogenicity to animals

A fungus which was identified by J. Ramsbottom as a species of *Paecilomyces* was reported by Ségal (1923) to induce in guinea-pigs a disease similar to typhus.

Turesson (1916) found *Pen. divaricatum* to be quite common in the human alimentary tract. When injected intravenously into rabbits it showed no pathogenicity, but feeding of spores and mycelium proved fatal.

P. burci (Poll.) Thom was isolated from a tumour in a woman (Pollacci, 1921). Dodge (1935) briefly described *Spicaria rubra* (Baquis) Dodge, which was isolated from lesions of the cornea, but which was not pathogenic to laboratory animals. Flood (1931) records that *P. varioti* gave a skin reaction in one asthmatic patient.

Occurrence on other fungi

P. marquandii (Massee) Hughes was isolated from the gills of *Hygrophorus virgineus* by Massee in 1897. *Spicaria mucoricola* Speg. (1899) was found on

a living *Mucor*. *S. penicillata* von Höhnel (1904) occurred on a Myxomycete *Arcyria punicea*. Petch (1936) described *S. simplex* as growing on *Trichia affinis*, and a specimen in his herbarium is a good *Paecilomyces*.

Occurrence on nematodes

Only one reference has been found relating to parasitism of eel-worms by a species of *Spicaria*. Drechsler (1941) described *S. coccospora* as actively parasitic on free-living nematodes.

Biochemistry

The number of biochemical studies carried out on species of *Paecilomyces* is small, compared with the enormous number of investigations of species of *Penicillium*.

Birkinshaw, Charles, Hetherington & Raistrick (1931 *a*), in a study of the metabolism of species of *Penicillium* by the carbon balance sheet method, included one strain of *P. varioti*. Later (1931 *b*) they included *Eidamia catenulata* (= *P. varioti*) amongst a miscellaneous collection of moulds which were studied by the same method. They said: 'The production of large amounts of volatile neutral compounds, with correspondingly high respiration coefficients, absence of volatile acids, production of moderate amounts of titratable acidity, together with moderate amounts of carbon in the form of non-volatile acids, and a moderate value for "carbon unaccounted for", all suggest the type of carbon balance sheet associated with *Aspergillus clavatus*, or with some strains of *A. niger*.'

Shaposhnikov & Manteifel (1923) reported the production of citric acid (at 40° C.) by a thermophilic mould described as a new species, *Pen. arenarium*. Thom (1930) regards this as probably a strain of *P. varioti*.

Sakaguchi *et al.* (1939) described two new moulds, *Monilia formosa* and *Pen. viniferum* (both now regarded as synonyms of *P. varioti*) and showed that they produced, amongst other substances, ethyleneoxide-α,β-dicarboxylic acid.

Raistrick & Smith (1933) reported the production from glucose by *Byssochlamys fulva* of a substance named byssochlamic acid ($C_{18}H_{20}O_6$), the structure of which has not yet been elucidated.

Thom & Raper (1932) isolated a strain of *Paecilomyces* on an arsenic-containing medium. When tested on Czapek agar containing compounds of arsenic it was found to be an active producer of gaseous compounds of arsenic.

Vora (1951) studied the metabolic products of *P. victoriae*, grown on Raulin-Thom medium. The metabolism solution, which gave a brownish purple with ferric chloride, yielded the following compounds: (1) ustic acid, a substance first isolated as a metabolic product of *Aspergillus ustus*; (2) dehydroustic acid, an oxidation product of ustic acid; (3) 4:6-dihydroxy-3-methoxy-phthalic acid; (4) a compound $C_9H_8O_5$.

Materials and methods

Cultures

The cultures used in this study were obtained from a variety of sources, but, during the investigation, have been kept as a separate collection, under numbers 'Pa 1 – '. In cases where cultures are duplicated in the collections maintained at the L.S.H.T.M., both numbers are cited in the lists of Material Studied.

We are particularly indebted to the Centraalbureau voor Schimmelcultures, Baarn, Holland, for supplying us with all the species of *Paecilomyces*, *Spicaria* and *Isaria* in that unique collection. These are denoted below by the abbreviation C.B.S. Other abbreviations are:

Ad. Part of a collection of mould cultures accumulated in the Research Department of Nobel's Explosives Co., Ltd., Ardeer, Ayrshire, and transferred to the L.S.H.T.M. in 1931.

A.T.C.C. The American Type Culture Collection.

B.B. Cultures, chiefly from cotton goods, collected in the laboratory of Messrs Boardman and Baron, Ltd., Great Harwood, Lancs, and transferred to the L.S.H.T.M. in November 1930. The collection has since been extended from other sources.

B.C.I.R.A. The British Cotton Industry Research Association, Shirley Institute, Didsbury, Manchester.

C.M.I. The Commonwealth Mycological Institute, Kew.

L.S.H.T.M. The London School of Hygiene and Tropical Medicine. 'P' and 'X' numbers refer to sections of this collection.

N.R.R.L. The culture collection of the Northern Regional Research Laboratory of the U.S. Department of Agriculture, Peoria, Illinois.

Culture media

The most useful media were Czapek agar, malt agar and potato agar. Cornmeal agar was suitable for a few species, and carrot extract agar, mixed carrot and potato agar, and macerated whole carrot with agar, were used from time to time.

Czapek agar was made to the usual formula, using KH_2PO_4 and 3 % sucrose.

Malt agar contained the salts of Czapek's medium together with 5 % of 'Vimaltol' and 2 % agar.

Potato agar contained a decoction from 200 g. potatoes, 20 g. glucose, and 20 g. agar per l. Carrot extract agar was similar except that only 50 g. carrot was used per l.

Cornmeal agar was made up with 60 g. finely ground maize per l.

Whole carrot medium was made with 300 g. carrot per l. The vegetable was boiled till tender in a small amount of water, put, along with the water, through a high-speed macerator, made up to volume, cooked with 1·5 % agar, tubed and sterilized. The medium is a bright orange when first made, but gradually fades to a pale dull pink, especially when kept in the light.

Cultural Methods

Stock cultures have been kept on agar slants in plugged tubes. These have been stored in a refrigerator at approximately +8° C., and transferred at about 4-monthly intervals. Each strain has been kept in duplicate on media which were known from experience to give good and typical growth. If at any time a strain appeared to be atypical or degenerating, cultures were grown on a variety of media, at different temperatures, and in both light and darkness, in the hope of restoring vigour. In most cases this was successful, but occasionally it was necessary to make sets of dilution cultures and reisolate from the most typical colonies. It was found to be unnecessary to resort to single spore cultures except with *Cordyceps militaris*. In this case cultures were obtained from single ascospores and part-spores, so that there should be no doubt about the connexion between the perfect and imperfect stages.

As with species of many other genera, it has been found that most of the species of *Paecilomyces* spore better in Petri dishes than in tubes or bottles. Most of the diagnoses have been drawn up mainly from Petri dish cultures.

Slide cultures were often useful, the agar block method of Duncan, described by Riddell (1950), being suitable for all species except *P. fumoso-roseus*, which grew atypically under these conditions. Cultures on cellulose sheet, as described by Fleming & Smith (1944), were used for observations on germinating spores, though these had to be substituted by plain agar surfaces for observing the germination of ascospores of *Byssochlamys*.

A complete study of temperature relationships of all species was not attempted. Representative strains of each species were grown on two media at 8° C. (refrigerator used for storage of cultures), 10–14° (vaults at L.S.H.T.M.), 24°, 30° and 37° C. It was unfortunate that, for this study, a steady temperature between 14° and 24° C. was not available as there is good reason to believe that the optima for some species lie in this region.

Observations on living cultures

Thom (1930) emphasized strongly that Penicillia cannot be described in terms which can be used by others for identifications unless as many observations as possible are recorded from living cultures. The same holds true to an even greater degree in *Paecilomyces*. Here there is more variation in a single species, and less difference between different species, in details of the sporing structures and in size, shape, and markings of spores.

All the strains were grown in Petri dishes, and examined at frequent intervals. Data recorded were: rate of growth as determined by measurements of colony diameters; depth of colonies; texture; type of margin; colour and colour changes; presence or absence of respiration drops; degree of sporulation; colour of reverse.

Microscopical methods

In all cases cultures in Petri dishes were examined directly on the stage of the microscope. Details of texture were made out in this way, also the disposition and overall dimensions of sporing structures. Habit sketches

were drawn at this stage, freehand against a scale and with a micrometer in the eyepiece. In most cases slide cultures were also used.

For slides made in the ordinary way lacto-phenol was used. Stains were either picric acid in the lacto-phenol or orseillin in acetic acid.

For measurements of sporing structures and spores both slides and slide cultures were used. A special $\frac{1}{12}$ in. objective was available, strictly corrected for a tube-length of 180 mm., it having been previously determined that, at this tube-length, one division of a micrometer in a $\times 15$ eyepiece was exactly equivalent to 1 μ. For high-power drawings a right-angled prism over the eyepiece was used to project a real image on to the paper.

TAXONOMY

PAECILOMYCES Bainier

Bainier's description of *Paecilomyces*, based on the single species *P. varioti*, tends to confuse generic and specific characters, and is certainly not adequate to include all the species which are discussed here. Thom's generic diagnosis (1930) is both more comprehensive and more concise. The following emended diagnosis is based on Thom's but is modified to cover all the species which are now regarded as belonging to the genus.

Paecilomyces Bainier. Genus related to *Penicillium* and *Gliocladium*, distinguished by phialides which are short tubular, or more or less swollen in the basal portion and tapering into long slender conidium-bearing tubes which are mostly curved or bent slightly away from the main axis of the cell; phialides variously arranged, partly in verticils and branching systems suggesting *Penicillium*, partly irregularly arranged upon short branchlets, partly sessile on and arising singly from the fertile hyphae; conidia in chains, but, in some species, especially when grown under very moist conditions, tending to slip sideways, or even to slime down into balls as in *Gliocladium*; colonies white, or pale coloured, or in dull brownish shades, occasionally with a greenish tone but never true green. Perfect state, where known, *Byssochlamys* Westling.

The colony

The vegetative growth tends to be more or less floccose. It may be comparatively thin, consisting of a matted web of aerial hyphae, or deeply floccose, loose or dense, or may be to varying degrees funiculose. Occasionally erect synnemata, or even true coremia, are formed, but these are rare in cultures made under ordinary conditions. A few species tend to produce wet and slimy colonies, especially in the early stages of growth.

Some species are persistently white, or white for some time but becoming slightly coloured as conidium production reaches its maximum. Others show definite colours in comparatively young cultures, but these colours are mostly pale and rarely at all greenish. There is, however, one species, *P. victoriae*, which is distinguished by its greenish tone, although colonies can hardly be described as true green.

Reverse colours of colonies vary considerably. The commonest shades are dirty white, dull buffs, and browns, but a few species produce dis-

tinctive and bright colours, which are an aid to identification, particularly of fresh isolates. Some isolates tend to lose these distinctive colours on continued cultivation.

Few species of the genus produce transpiration drops, which are such a marked feature of many species of *Penicillium*, and none has so far been found to have more than a slight odour.

Sporing structures

The conidiophores. These, when present, arise mostly from trailing aerial hyphae or funicles of hyphae. Occasionally they are united in small coremia. They vary greatly in length, but seldom exceed 500 μ. They are septate, except when very short, and may be of uniform diameter or, particularly in *P. varioti*, tend to be enlarged below each septum. The diameter varies considerably from species to species, averaging 0·8 μ in *P. farinosus* and ranging up to 8 μ in *P. elegans*. There is rarely any roughening of the conidiophores, such as is fairly common in *Penicillium*. In all species sporing structures which lack definite conidiophores are common, and in a few species well-defined conidiophores are rarely formed.

The sporing head. In most species all types of sporing head, from complex to the simplest possible, are to be found, though usually one type predominates in each species.

The simplest sporing structures consist of single phialides, or small clusters of phialides, borne directly on vegetative hyphae. Monoverticillate heads, consisting of a definite conidiophore bearing a single whorl of phialides, are common. In these the tip of the conidiophore is usually somewhat swollen. More complex forms may consist of 'penicilli', strongly reminiscent of the Asymmetrica group of *Penicillium*, but more usually consist of successive whorls of phialides, or of phialides and prophialides (metulae), along a main axis, or of loose tree-like branching systems.

The Phialide. In *Paecilomyces* the phialide is very characteristic. The basal portion may be roughly cylindrical, but is more often somewhat narrowed at the point of attachment to the parent branch, and is commonly a little over half the total length. It tapers gradually or abruptly to a long slender tube, which is usually bent away from the main axis of the cell. The unusual length of the phialides, the slenderness of the terminal portion, and the characteristic bend, together form one of the chief distinguishing features between this genus and *Penicillium*. A further point of distinction is that in *Paecilomyces* the phialides in a whorl are markedly divergent, whereas in most species of *Penicillium* they tend to form a compact cluster.

The Conidium. The conidia are formed within, and are extruded from, the tips of the phialides. In some strains this endogenous origin of the conidia is readily seen. They are one-celled, hyaline under the microscope but often pale coloured in mass, mostly smooth but occasionally finely roughened, usually ovate, elongate, or almost cylindrical, but in one or two species almost spherical.

The conidia are normally dry and borne in long, often very long, chains. Owing to the phialides being mostly divergent, the chains, although far from straight, are seldom tangled, as in many species of

Penicillium. If colonies are growing in a very moist atmosphere the conidia in the chains may slip sideways, so that the long axis lies across or diagonally to the main axis of the chain. In a few species the slipping of the conidia goes a stage further, giving rise to irregular masses of spores. The phenomenon is often observed in slide cultures which are incubated in a nearly saturated atmosphere, but even here it tends to occur with some species much more readily than with others. This incipient sliminess of the conidia obviously links *Paecilomyces* with *Gliocladium*.

Macrospores. Many isolates of the common *P. varioti*, and also of some other species, produce large thick-walled cells, which are usually termed 'macrospores'. It was the presence of these cells which led Horne & Williamson (1923) to classify *P. varioti*, along with *Trichoderma viride*, in the genus *Eidamia*. The macrospores are most often terminal, and are then typical aleuriospores. They are mostly subglobose to pyriform. Less frequently they are intercalary, and are then more often barrel-shaped. Their dimensions vary greatly in a single species and even in a single isolate.

Raper & Thom (1949) make a curious statement regarding these structures, as follows: 'Their significance soon became apparent when Olliver & Smith (1933) discovered a strain presenting the general morphology of *P. varioti* in all respects except that these sterile cells, or macrospores, developed into individual asci....' This seems to imply that Olliver & Smith suggested that this transformation occurs, which is certainly not the case. Ascus formation in both species of the genus *Byssochlamys* is preceded by the development of a spiral, which eventually becomes not a single ascus but a whole cluster of asci. In no case is there any stage in the process which remotely resembles a macrospore.

BYSSOCHLAMYS Westling

The author's diagnosis is adequate, and (translated) reads: 'Mycelium floccose, snow-white, creeping; hyphae plurinucleate. Peridium nil; asci naked, subsessile, conglomerate, 8-spored. Chlamydospores formed singly at the ends of hyphae. Conidia in chains; basidia short, usually simple.'

It was suggested by Thom (1930) that Westling's genus is related to *Paecilomyces*. This became evident when Olliver & Smith (1933) described *B. fulva*, with a conidial state practically indistinguishable from *P. varioti*.

The colony

The appearance of the colony depends a good deal on the relative abundance of asci and conidial structures, and this in turn depends on the temperature at which the colony is grown. At temperatures of 30° C. or over, when asci are predominant, the colony is whitish and granular, with little floccose aerial growth. At lower temperatures, 24° C. or lower, conidial production is enhanced and, particularly in the case of *B. fulva*, the general aspect is typical of *Paecilomyces*, with a somewhat dense layer of clusters of asci underneath the funiculose aerial growth.

The imperfect state is definitely *Paecilomyces* and needs no further description here.

Ascus formation

Westling (1909) described ascus formation in *B. nivea* as follows: 'The formation of asci commences by the swelling of a hypha, either at the tip or at a septum, to a diameter of 5–12 μ. The protuberance is delimited by a septum and, from an adjacent hyphal branch, one or more slender hyphae (the ascogonium) grow out and twist round the central antheridium. . . . In addition one frequently finds an arched or somewhat coiled ascogonium put out by the ascogenous hyphae, without being able to find an antheridium in the vicinity'.

Emmons (1935) reported on ascus formation in *B. fulva* thus: '*Byssochlamys fulva* has a short hyphal coil from which the ascogenous hyphae arise, and through the intervention of croziers naked asci develop.'

Ascus development has been followed in both *B. nivea* and *B. fulva*. The process is the same in the two species and, apart from the fact that no structures have been found which could be interpreted as antheridia, the early stages of the process are as described by Westling and Emmons. Asci are formed in irregular clusters of indefinite size; they are globose to subglobose or ovate, and 8-spored.

Ascospores

The ascopores are one-celled, hyaline, broad ellipsoidal and smooth. They show no trace of the median furrow which is such a noticeable feature of the ascospores of the *Aspergillus glaucus*, *fischeri*, and *nidulans* groups. The *Aspergillus* spore appears to consist of two symmetrical valves, with an exospore which may be smooth, but is more frequently thrown up into crests or frills along the edges of the valves, and sometimes into roughening of the whole surface of the spore. At germination the exospore splits along the line of contact of the two valves, that is along the furrow between the two frills. The separated halves of the exospore can often be seen lying on opposite sides of the germinated spore.

In *Penicillium* the bivalve type of ascospore is rare. The exospore may be smooth or form roughenings or ridges of varying complexity, but the general contour of the spore is ellipsoid. In *Byssochlamys* the spores are most like those of the Penicillia, regularly ellipsoid. They germinate from any part of the surface.

Key to species of *Byssochlamys* and *Paecilomyces*

The primary basis of separation of species of *Paecilomyces* is colony texture. Three main groups are recognized: Funiculosi, with colonies markedly funiculose, bristly, or coremiform; Floccosi, with colonies densely floccose, filling culture tubes, or forming fairly thick, cushion-like hyphal conglomerates; and Compacti, with colonies comparatively thin, usually consisting of densely matted mycelial felts, but occasionally very thin and sparse. Whilst it is true that nearly all species of the Floccosi and Compacti show some tendency to produce hyphal ropes in old cultures, it is considered that the suggested classification is a workable one for species

identification, since the differences in texture are quite clear-cut during the rapidly growing period.

A number of species which have not been studied in culture are included in the key. The disposition of these is, of course, provisional only.

1. Asci produced. Genus **Byssochlamys** 2
   Asci not produced. Genus **Paecilomyces** 3
2. Colony colour persistently white. **B. nivea** (p. 35)
   Colony colour partly or predominantly fulvous. **B. fulva** (p. 37)
3. Colonies markedly funiculose, tufted, or definitely coremiform. **FUNICULOSI** 4
   Colonies deeply floccose or forming convex cottony cushions; isarioid forms occasionally produced in fresh isolates. **FLOCCOSI** 11
   Colonies comparatively thin, matted or sparse **COMPACTI** 15
4. Conidial heads predominantly complex. 5
   Conidial heads simple or complex, but if the latter loose in structure; conidia large, up to 10 μ long, rough. **P. herbarum** (p. 43)
   Conidial heads mostly simple. 9
5. Conidia in mass avellaneous to fulvous. **P. varioti** (p. 40)
   Conidia in mass white. 6
6. Conidia large, 4–8 μ in long axis, fusiform or long oval, sometimes borne obliquely in chains. 7
   Conidia small, less than 4 μ, always in normal chains. 8
7. Conidia 7–8 × 4–5 μ; forming coremia on insects. **P. smilanensis** (p. 76)
   Conidia 4–6 × 1·5–3 μ; reverse of colony usually brownish, but occasionally pink to crimson. **P. elegans** (p. 47)
8. Colonies partly floccose and partly coremiform; conidia 2–3 × 1–1·8 μ. **P. farinosus**—fresh isolates only (p. 50)
   Growth on insects funiculose; conidia 2·5–3·2 × 1·8–2·2 μ **P. simplex** (p. 76)
   Growth on insects coremiform; conidia 2–2·5 × 1–1·5 μ. **P. longipes** (p. 75)
9. Conidia large, up to 8 μ, fusiform, with spiral ridges or reticulate. **P. fusisporus** (p. 45)
   Conidia small, not exceeding 5 μ, smooth. 10
10. Colonies dirty white; macrospores abundant; conidia tardily produced, fusiform, 3–5 × 1·5–2 μ. **P. puntonii** (p. 54)
    Colonies tardily pale clear yellow, tufted; conidia ovate, 3·5–4 × 2–2·5 μ. **P. flavescens** (p. 56)
    Colonies greyish to avellaneous; conidia globose, 4–5 μ diam. **P. burci** (p. 73)
    Colonies slimy at first, tardily funiculose; conidia subglobose, 2·5–3 μ diam. **P. parvus** (p. 58)
11. Colonies white at first, but often becoming tinted in age. 12
    Colonies purplish or violet. 14
12. Colonies persistently white or becoming yellowish in age. **P. farinosus** series 16
    Colonies becoming pale grey-green; conidia ovate, 2·2–3·1 × 1·4–2 μ. **P. victoriae** (p. 60)
    Colonies becoming pale bluish grey; conidia fusiform, 4–6 × 1–1·5 μ. **P. javanicus** (p. 65)
    Colonies becoming pinkish or rose. 13
13. Colonies becoming rose-coloured; conidia 6·5–10 × 5–6 μ. **P. fimetarius** (p. 75)
    Colonies dense floccose, tardily pinkish; conidia 3–4 × 1–2 μ. **P. fumoso-roseus** (p. 67)
14. Colonies becoming violet; reverse intense yellow. **P. marquandii** (p. 62)
    Colonies sordid vinaceous; reverse vinaceous or purple. **Penicillium lilacinum** (p. 64)
15. Colonies restricted, cushion-like, tardily becoming pale pink; reverse on Czapek agar intense green; conidia slightly rough. **P. carneus** (p. 70)
    Colonies very thin, restricted, often slimy, but eventually more or less funiculose. **P. parvus** (p. 58)

16. Conidial chains often sliming down to form spore balls or irregular masses. **Cordyceps militaris** st. conid. (p. 53)
Conidial chains mostly dry. **17**
17. Conidia globose, small. **P. coccosporus** (p. 74)
Conidia ellipsoidal. **18**
18. Conidia $2–3 \times 1–1·8\,\mu$. **P. farinosus** (p. 50)
Conidia $3–4 \times 1·5–1·8\,\mu$. **P. cossus** (p. 74)
Conidia $4–5·4 \times 2·8–3\,\mu$. **P. canadensis** (p. 74)
Conidia $5–7 \times 3–3·5\,\mu$. **P. heliothis** (p. 75)

Descriptions of species of *Byssochlamys* and *Paecilomyces* which have been studied in culture

BYSSOCHLAMYS Westling

Byssochlamys nivea Westling (1909), p. 134, Taf. 4 (Text-fig. 1)

Colonies on Czapek agar at 30° C. spreading rapidly, covering a Petri dish in 7 days, consisting at first of a loosely floccose to funiculose mat, becoming a densely matted felt with some loosely funiculose tufts, dying down in age and appearing almost granular, with margin thin and arachnoid during the growing period, white to just off white; drops lacking at first, then appearing sparsely, large, colourless; odour none at first, then faintly mouldy; reverse white, becoming faintly yellowish; conidial structures sparse, but when present similar to those on malt agar; asci numerous, conglomerate, globose to subglobose, $8·5–10·5 \times 7·5–9·5\,\mu$, 8-spored; ascospores smooth, regularly ellipsoid, $5–5·6 \times 3·2–3·8\,\mu$; typical aleuriospores (macrospores) fairly abundant, smooth, $4–7 \times 2·5–5\,\mu$.

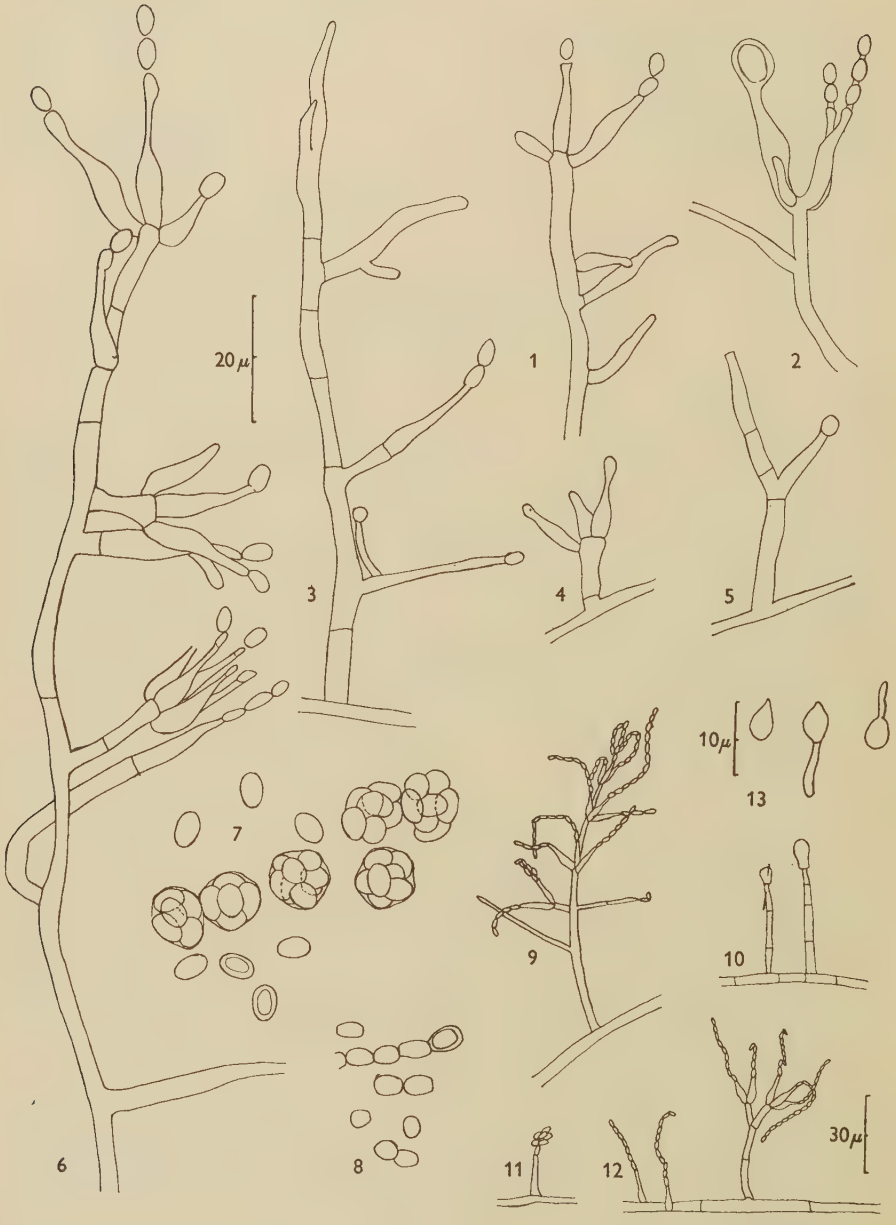
Colonies on malt agar at 30° C. similar to colonies on Czapek, but growing rather more rapidly and somewhat more deeply floccose when young; conidial structures usually evident, the more complex ones consisting of several whorls of phialides, or mixed phialides and branches, borne at successive nodes along the conidiophore, but all types produced, from these comparatively complex heads to single phialides borne directly on trailing hyphae; conidiophores, when present, $15–300\,\mu$ long and $2–3\,\mu$ diam., sometimes branched; phialides with swollen base and tapering at about half the length to a long thin tube about $1\,\mu$ in diam., very variable in length, $8–19\,\mu$, and $1·6–3\,\mu$ diam. at the broadest part; conidia smooth, broad ellipsoid, often with one end slightly flattened, $3·8–6 \times 2·5–5\,\mu$; aleuriospores present but not abundant; asci and ascospores as on Czapek agar.

Colonies on potato agar at 30° C. similar to those on Czapek except that conidial structures are somewhat more abundant.

On all media growth is better and more typical at 30° C. than at 24° C. Hence the above diagnosis has been drawn up from cultures grown at the higher temperature.

Conidia germinate usually by a single germ-tube. Ascospores swell to about $8 \times 6\,\mu$, then put out one or two germ-tubes, which are usually produced terminally but are sometimes lateral.

Growth is very slow at temperatures below 20° C., is fairly rapid at 24 °C., and very rapid at 30–37° C.



Text-fig. 1. *Byssochlamys nivea*. 1–6, conidial structures, showing range of pattern; 7, asci and ascospores; 8, conidia; 9–12, habit sketches of conidial structures and macrospores; 13, germinating ascospores.

Occurrence

Only three records can be traced. Westling (1909) found it on specimens of *Geastrum* from which the preserving spirit had gradually evaporated. J. H. Warcup isolated it from soil in 1950 (personal comm.). Chesters also, at a Brit. mycol. Soc. meeting in March 1953, reported it from soil.

Material studied

Pa 26. Culture from J. H. Warcup, received Feb. 1950. Isolated from soil, Clophill, Beds.

Byssochlamys fulva Olliver et Smith (1933), p. 197, pl. 602, figs. 1, 2 (Text-fig. 2)

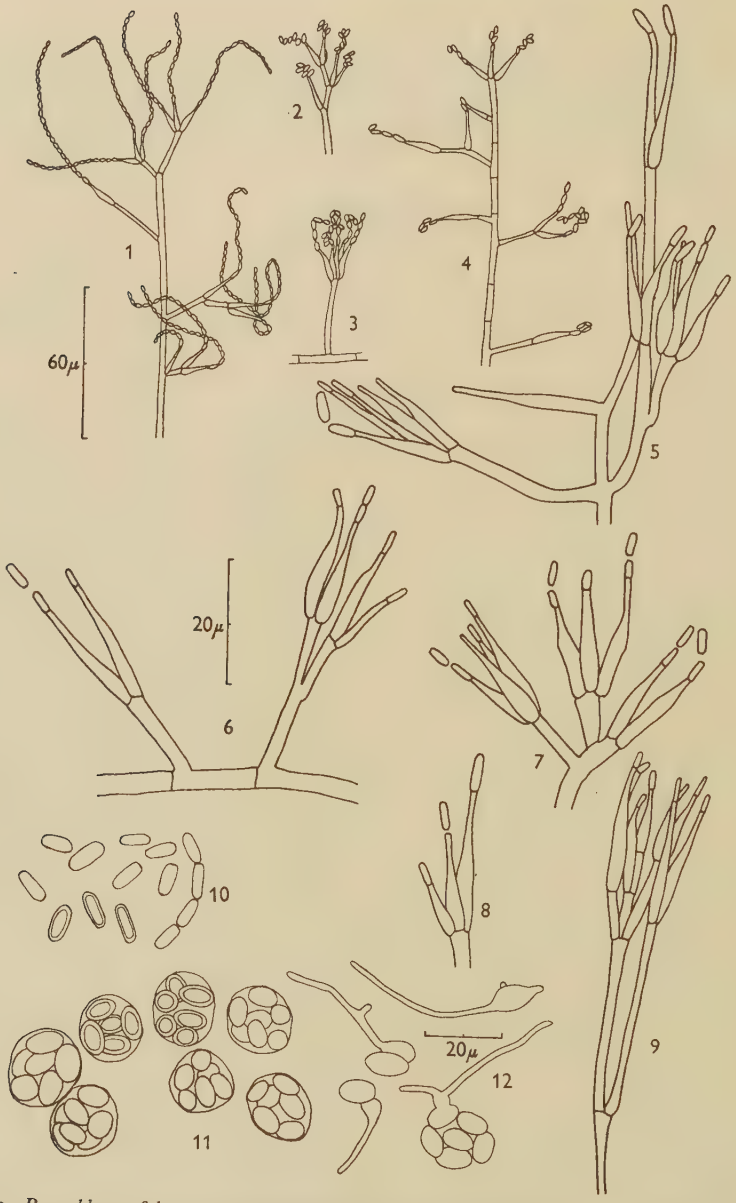
Byssochlamys musticola Naumoff et Kiryal. (1935), p. 362.

Colonies on Czapek agar spreading rapidly, covering a Petri dish in 7 days, 0·5–1 mm. deep at 24° C. and 1–2 mm. at 30° C., consisting at first of a very thin basal felt with a fine funiculose overgrowth, becoming a densely matted floccose or funiculose felt with a loose funiculose overgrowth, later developing granular patches (asci), with margin thin and arachnoid during the rapidly growing period, pale yellowish buff or tawny to snuff brown; exudate lacking or limited to a few colourless drops; reverse pale dull yellowish or brownish; sporing structures varying in complexity from single phialides borne directly on aerial hyphae to loose irregularly branched heads with branches terminating in single phialides, whorls of phialides, or mixed whorls of phialides and further branchlets; conidiophores arising from aerial hyphae or ropes of hyphae, usually short, up to about 100 μ, but occasionally up to 500 μ long, 2–4 μ diam., smooth, septate; phialides up to 5 in a whorl, with more or less cylindrical or swollen basal portion, tapering gradually for about half their length to a long thin tube which is often bent, 8–25 μ long and 1·4–3·5 μ diam. at the broadest part; conidia ovate to cylindrical or barrel-shaped, smooth, 4–9 × 1·5–3 μ, in very long twisted, divergent or loosely tangled, chains; asci conglomerate, 8-spored, subglobose, 10–13 × 9–12 μ; ascospores regularly ellipsoidal, smooth, 5·5–7 × 3·5–4·5 μ, mostly 6·5 μ long.

Colonies on malt agar growing somewhat more rapidly than on Czapek, and becoming somewhat deeper and more funiculose. Otherwise findings are as on Czapek.

Colonies on potato agar as on Czapek except that they are usually slightly more definitely funiculose. Details of conidial structures and asci as on Czapek.

As in the case of *B. nivea* growth is more rapid and typical at 30° C. than at 24° C. Hence the above diagnosis is drawn up from cultures incubated at the higher temperature. If successive subcultures are always grown at 24° C. or lower temperatures they tend to become entirely conidial, and the ability to produce asci is permanently lost. Production of asci can be ensured by growing cultures at any temperature between 30 and 37° C. for 10–14 days. Afterwards they may be stored at any convenient temperature.



Text-fig. 2. *Byssochlamys fulva*. 1–4, habit sketches of conidial structures; 5–9, conidial structures; 10, conidia; 11, asci; 12, germinating ascospores.

Conidia swell and often become grotesquely shaped before germination, then put out one germ-tube, sometimes followed by another after some delay. Ascospores germinate by a single germ-tube issuing from any point on the spore wall.

Growth is slow to very slow at temperatures below 20° C., good at 24° C. but, as stated above, tending to be predominantly or entirely conidial, and very rapid at 30–37° C.

Occurrence

This species was originally isolated from bottled fruit, and at one time it created a serious problem in the fruit-preserving industry. It was later shown by Olliver & Rendle (1934), Gillespey (1938, 1941), and Hull (1939) to be a fairly common organism in orchard soils in England. According to Raper & Thom (1949) it is uncommon in America, and, so far as is known, it has not been reported from any other country, except possibly as *B. musticola* from U.S.S.R. (see below).

Physiology

B. fulva shows unusual resistance to a number of influences which are lethal to most fungi. It can grow at low oxygen tension—hence its ability to grow in cans and bottles of preserved fruit; it can tolerate up to 50 parts per million of SO_2 in saline and plum syrup, and up to 450 p.p.m. in a solution containing 10% sucrose and 1% peptone; it is not killed by ammonia liberated from 2·5 ml. of concentrated ammonia per litre, or by 1:200 acetaldehyde; the ascospores can survive a temperature of 84–87° C. for 30 min. in saline or syrup and, in experiments in which syrup containing ascospores was heated at the same rate as the cans in normal processing, the spores retained their viability until a temperature of 98° C. was reached; the spores can also withstand immersion in absolute alcohol for 30 weeks at least (Olliver & Rendle, 1934). It is interesting that Westling reported unusual resistance to lethal influence in his *B. nivea* and that the fungus was several times isolated from specimens from which the preserving alcohol had gradually evaporated.

The description of *B. musticola* Naumoff et Kirjal. is inadequate, but, apart from unusual variation in size of ascospores, it would fit *B. fulva*. Unless and until cultures become available and it is definitely shown that the two are different, it is probably best to regard *B. musticola* as a synonym of *B. fulva*.

Material studied

Pa 24. (=B.B. 134.) Culture from T. Rendle of Messrs Chivers and Co., Histon, Cambridge, Jan. 1933. The original isolate from bottled fruit on which the new species was erected. Is now typical *P. varioti*, since it no longer produces any asci.

Pa 25. (=B.B. 134*a*.) Isolated from soil at Long Ashton and received from S. C. Challinor, May 1947. Is still quite typical.

Pa 29. (=X. 6*a*.) Isolated from soil near Cambridge and received from T. Rendle, Oct. 1934. Production of asci is somewhat sparse; otherwise typical.

Pa 22. (N.R.R.L. 1125.) Culture received from K. B. Raper, July 1948. Typical but production of asci tardy.

PAECILOMYCES Bainier

Section *FUNICULOSI*

PAECILOMYCES VARIOTI Bainier (1907), pp. 26–7, pl. VII (Text-fig. 3)

Penicillium divaricatum Thom (1910), p. 72, fig. 29.
Corollium dermatophagum Sopp (1912), pp. 98–103, Taf. X.
Spicaria elegans (Corda) Harz var. *flava* P. Sée (1919), p. 33, pl. I, figs. 3–8.
Pen. mandschuricum Saito (1921), pp. 11–12.
Pen. aureo-cinnamomeum Biourge (1923), p. 213.
?*Pen. arenarium* Shaposhnikov et Manteifel (1923), p. 3.
Eidamia catenulata Horne et Williamson (1923), p. 398, figs. 7–13.
Paecilomyces mandshuricus (Saito) Thom (1930), p. 550.
Spicaria divaricata (Thom) Gilman et Abbott (1927), p. 301.
P. aureo-cinnamomeus (Biourge) Thom (1930), p. 547.
Spicaria divaricata (Thom) Ma (1933), p. 115 (a later homonym).
P. mandshuricus (Saito) Thom var. *saturatus* Nakazawa, Takeda et Suematsu (1934), p. 102.
?*Spicaria taurica* Naumoff et Kiryal. (1935), p. 363.
Monilia formosa Sak., Inoue et Tada (1939), p. 302.
Pen. viniferum Sak., Inoue et Tada (1939), p. 303.

Colonies on Czapek agar at 24° C. growing fairly rapidly, but showing considerable variation between different strains in rate of growth, attaining a diameter of 35–60 mm. in 7 days and covering a Petri dish in 10–14 days, consisting of a matted basal felt with loose floccose funiculose overgrowth, with margin either narrow and abrupt or broad and arachnoid, ochraceous, shading through pale yellow to white at the margin, becoming deeper and duller in colour, dirty yellowish buff, often with a greenish or pinkish tinge; drops occasionally present, sparse, colourless; odour at first nil, after 7–10 days sweet aromatic; reverse usually dirty yellow, buff, or pale brown, occasionally with greenish tones; fruiting structures very variable, ranging from solitary phialides to complex heads with several stages of branching, but with the latter usually irregular, consisting of whorls of phialides mixed with secondary branches; conidiophores arising from aerial hyphae or ropes of hyphae, often lacking, normally 90–200 × 2·5 μ, but varying from 15 to 900 μ long and 1 to 3 μ in diameter, sometimes with local swellings up to 6 μ diam., and usually swollen at the apex to 4–5 μ when bearing a monoverticillate head; phialides up to 7 in a whorl, with cylindrical basal portion and tapering at a little over half the length to a long slender tube about 1 μ in diam., usually bent more or less sharply, very variable in size, 8–25 μ long and 1·5–2 μ diam. at the broadest part; conidia smooth, ellipsoid to cylindrical, 3–6 × 1·5–3 μ, mostly 4–5 × 2–3 μ; macrospores produced by some strains, terminal and resembling aleuriospores or intercalary in hyphae or even in phialides, globose to ovate, 8–10 × 4·5–8 μ.

Colonies on malt agar at 24° C. usually growing more rapidly than on Czapek, 50–60 mm. diam. in 4 days and covering a dish in 7 days, but occasional strains growing at same rate as on Czapek; reverse in deeper and more orange shades than on Czapek; in all other respects similar to colonies on Czapek.

Colonies on potato agar growing somewhat more rapidly than on Czapek, becoming 65–80 mm. diam. in 7 days and covering a dish in

10 days, with aerial growth more funiculose; sporing structures often slightly larger than on Czapek, with conidia up to 7 μ long.

Conidia swell irregularly and become distorted before germinating. Two successive germ-tubes are normally produced.

Text-fig. 3. *P. varioti.* 1–6, conidial structures; 7–9, habit sketches of conidial structures; 10, macrospores *in situ*; 11, conidia; 12, macrospores.

Growth is slow at 15° C. or lower and nil at about 8° C.; it is rapid at 24° C. and very rapid at 30° C. and up to 37° C.

Discussion

P. varioti is a very variable species and, in consequence, has been described under a variety of names. The above diagnosis is drawn from a study of what may be termed typical isolates. Occasional strains grow comparatively restrictedly, or remain very pale coloured, but, even with these, there is no doubt as to their identity.

Of the synonyms given above *Pen. divaricatum*, *Corollium dermatophagum* and *Eidamia catenulata* have been discussed earlier. *Pen. mandshuricum* was adequately described by Thom (1930), who had seen Saito's isolate. *Pen. aureo-cinnamomeum* was considered by Thom (1930) as possibly distinct from *P. varioti*. Raper & Thom (1949), however, are inclined to regard it as synonymous with *P. varioti*, an opinion which, on the basis of Thom's data, we share. No material is now available, but Thom's description of a culture from Biourge, and Biourge's own diagnosis, suggest nothing that would distinguish it from *P. varioti*. *Pen. arenarium* is probably *P. varioti*, although the diffuse description includes unusual colours and dimensions (see Thom, 1930). *Spicaria elegans* var. *flava* is known only from description. It is definitely not related to *P. elegans* and, judging from the diagnosis and figures, is almost certainly *P. varioti*. *S. taurica* cannot be identified with certainty without cultures or herbarium material, but the very brief Latin diagnosis definitely suggests *P. varioti*.

Occurrence

This species is common and cosmopolitan, and occurs on a wide variety of substrata. It is therefore surprising that it was not described before 1907, since there is no lack of subsequent records. However, no earlier description which would fit this species has so far been traced. Its economic importance has already been discussed.

Material studied

Pa 1. Isolated from mouldy filter-paper, L.S.H.T.M., Oct. 1950. In every way typical.

Pa 4. Culture from C.B.S., received Nov. 1950, as *P. mandshuricus* (Saito) Thom var. *saturatus* Nak., Tak. et Suem., contributed by Nakazawa. This isolate is definitely *P. varioti*. It produces a loose funiculose type of colony, with abundant macrospores.

Pa 7. Culture from C.B.S., Nov. 1950, as *P. varioti*, C.B.S. isolate. It is quite typical.

Pa 8. (=Ad 44.) Received (at Ardeer) from C.B.S., Sept. 1925, as *Pen. divaricatum* Thom. Although this strain has been maintained in laboratory culture for at least 30 years it is still typical.

Pa 9. (=Ad 103.) Received (at Ardeer) from A.T.C.C., Nov. 1927, as *P. varioti* no. 1139. Produces typical colonies with somewhat sparse macrospores.

Pa 11. (=B.B. 122.) Culture from B.C.I.R.A., July 1930, as *Paecilomyces* sp., isolated from cotton yarn. Gives typical colonies with abundant macrospores.

Pa 12. (=B.B. 124.) Culture from B.C.I.R.A., July 1930, as *Paecilomyces* sp. from cotton yarn. Growth not quite so luxuriant as shown by most strains, but quite typical and producing a fair number of macrospores.

Pa 13. Culture from N.R.R.L., Dec. 1943, as *P. varioti*, N.R.R.L. 1118. Produces colonies normal in every way.

Pa 14. Culture from N.R.R.L., July 1948, as *P. varioti*, N.R.R.L. 1115. Colonies comparatively thin and no macrospores produced.

Pa 17. (=B.B. 62.) Isolated from cotton yarn, Mar. 1927, and originally identified as *Spicaria* sp. Colonies pale yellowish to pinkish buff, dense funiculose; many macrospores.

Pa 18. (=P. 219.) Culture from N.R.R.L., Apr. 1946, as *Pen. viniferum* Sak., Inoue et Tada, N.R.R.L. 1123. Rather slow growing, very thin at first, but eventually producing typical colonies; no macrospores.

Pa 31. (=X. 26.) Culture from N.R.R.L., Apr. 1946, as *Monilia formosa* Sak., Inoue et Tada, N.R.R.L. 1282. Pale colonies, pinkish buff to almost cream; some macrospores.

Paecilomyces herbarum sp.nov. (Plate 2, figs. 1, 2; Text-fig. 4)

Coloniae in agaro Czapekii lentissime crescentes, tenues, humidae, per quattuor hebdomades conidia non gerentes.

Coloniae in agaro 'malt' dicto lente crescentes, tenues, primum humidae, deinde mycelium aetherium tenue candidum sensim proferentes, per quattuor hebdomades conidia non gerentes sed aliquando in senectute conidiophoras typicas gerentes.

Coloniae in agaro 'potato dextrose' dicto vel in carota disintegrata cum agaro celeriter sed tamen lente crescentes, densae, primum vinaceae aut sub-brunneae, deinde hyphis fasciculatis sub-candidis, quae conidia lente efferunt, contextae; reverso inaequaliter brunneo; coloniae veteres, praecipue in 'carrot agar', sulcatae, zonatae.

Conidiophora plerumque brevia, sed aliquando ad 100 μ longa, fasciculata, irregulariter ramosa, plerumque 3 μ diam.; phialides in verticillatis, sed nonnumquam solitariae, 20–30 μ longae, cum basi 3–4 μ diam. et apice asperulo 1–1·3 μ diam.; conidia irregulariter ellipsoidea, saepe in uno extremo truncata, sub-asperula, (7) 8–9·5 (11) × 3–3·8 μ, in catenis longis implicatis.

Habitat in calamis mortuis herbarum, Anglia.

Colonies on Czapek agar at 24° C. growing very slowly, 8 mm. diam. in 12 days, thin, wet, transparent, not showing any sign of sporing after 4 weeks' incubation.

Colonies on malt agar growing better than on Czapek but still slowly, 15–16 mm. in 12 days, thin, wet at first but gradually developing whitish aerial growth, not usually sporing after 4 weeks' incubation, but sometimes producing normal conidiophores in very old cultures.

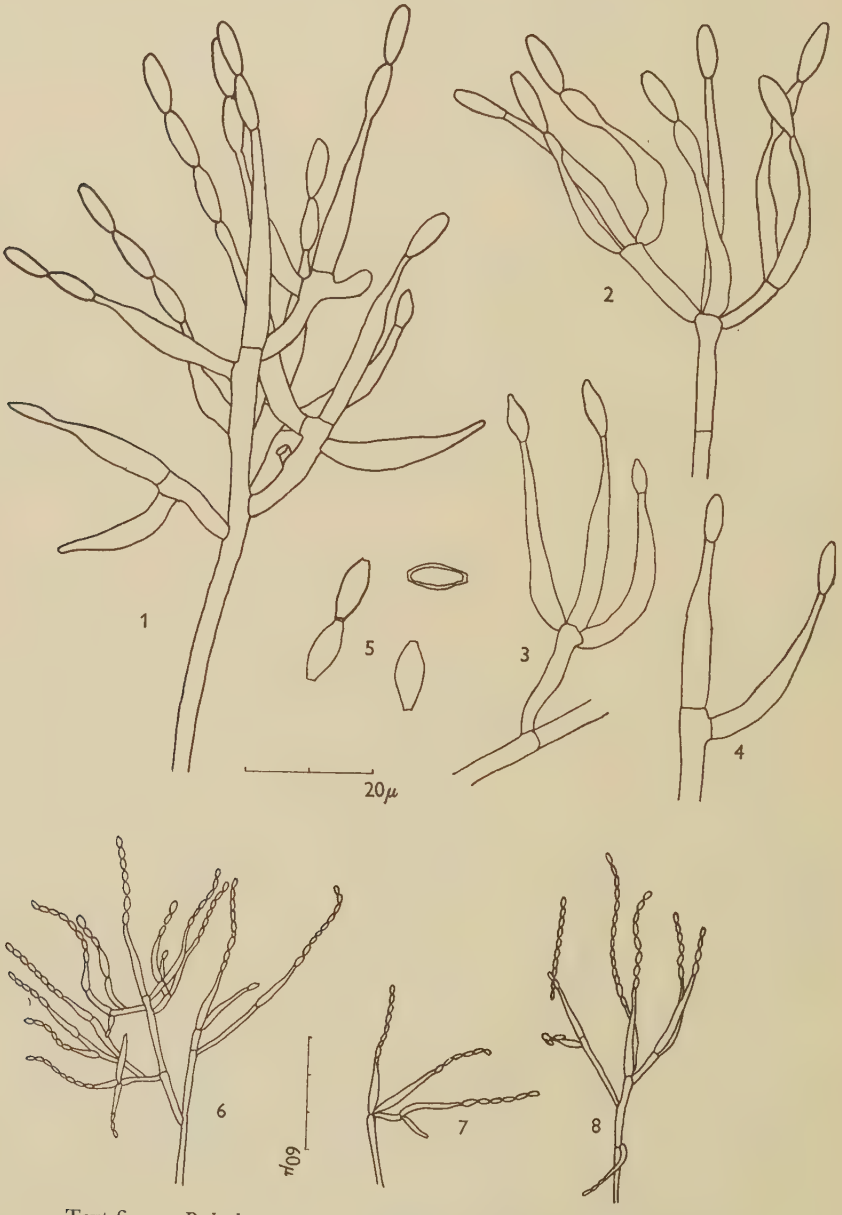
Colonies on potato-dextrose agar or disintegrated carrot agar growing somewhat better than on malt agar, 7 mm. in 6 days, 16–20 mm. in 12 days, forming pinkish to vinaceous or brownish mycelium close to the substrate, with white tufts slowly covering most of the surface, but usually deeply sulcate zonate, the tufts gradually becoming powdery as spores are formed, eventually dirty white to slightly brownish and powdery all over; reverse irregularly brown.

Conidiophores mostly short but up to 100 μ long, usually fasciculate, irregularly branched, seldom more or less verticillate, smooth, mostly 3 μ diam.; phialides usually in irregular verticils of 2–4, but sometimes solitary, sometimes mixed with metulae, 20–30 μ long and 3–4 μ diam. at the base, tapering rather gradually from about two-thirds the length to a slender tube 1–1·3 μ diam., often rough towards the apex; conidia irregularly ellipsoid, frequently truncate at one end, finely roughened, (7) 8–9·5 (11) × 3–3·8 μ, borne in long tangled chains.

In its natural habitat, on old stems of herbaceous plants, forms a thin funiculose mycelium close to the substrate, with funiculose aerial tufts,

white to cream; sporing structures very similar to those produced on artificial media but phialides occasionally longer, up to 40 μ, and of somewhat greater diameter, up to 5 μ.

Conidia germinate very slowly. Spores from a 3-month-old culture on



Text-fig. 4. *P. herbarum*. 1–4, conidial structures; 5, conidia; 6–8, habit sketches of conidial structures.

carrot agar, sown directly on to the surface of fresh carrot agar, showed no sign of germination, or even swelling, after 30 hr. After 40 hr. most of the conidia had enlarged slightly in width and a high percentage had produced germ-tubes, but even after 3 days some of the conidia were just showing first signs of germination. The germ-tubes are formed from any part of the surface of the spore, but are most often polar. Two germ-tubes are usually produced, most often successively but occasionally simultaneously, and a very small proportion of the spores produce three.

This species has a rather narrow temperature range. There is no sign of growth in 4 weeks at 0° C., but normal growth occurs when the inoculated plates are transferred to room temperature. At 8° C. growth is very slow, scarcely visible in 2 weeks and only 15–20 mm., on potato or carrot agar, in 10 weeks. At temperatures 15–24° C. growth is normal, and variations in temperature within this range have little effect on the rate. There is no growth at 30° C. and the conidia and mycelium are apparently slowly killed at this temperature, since plates incubated for 4 weeks at 30° C. and then transferred to room temperature show no sign of growth.

Material studied

Pa 63. Culture received from C.M.I., Jan. 1954, as '*Paecilomyces* Taxonomic sp. I, I.M.I. 53581'. It was isolated from stems of *Urtica dioica*.

The following six specimens in Herb. I.M.I. were all contained in the folder 'Paecilomyces Taxonomic sp. I'.

Herb. I.M.I. 19107, on dead stem of *Heracleum*, Exeter, 13 Sept. 1947. Collected by S. J. Hughes.

Herb. I.M.I. 19108, on dead petioles of *Gunnera scabra*, Exeter, 15 Sept. 1947. Collected by Miss E. M. Wakefield.

Herb. I.M.I. 19221 (e), on petioles of *Petasites ovatis*, Masham, Yorks, 13 Oct. 1947. Collected by S. J. Hughes.

Herb. I.M.I. 19559, on Umbelliferae indet., Ranmore Common, 2 Nov. 1947. Collected by S. J. Hughes.

Herb. I.M.I. 20036 (*a*), on *Heracleum sphondylium*, Ranmore Common, 14 Dec. 1947. Collected by S. J. Hughes.

Herb. I.M.I. 31407 (e), on dead stem of *Urtica dioica*, Masham, Yorks, 26 Sept. 1948. Collected by S. J. Hughes.

All the specimens were obviously the same species, and measurements agreed with those taken from cultures of Pa 63. The species is apparently widely distributed on dead herbaceous stems, but is not common.

Herb. I.M.I. 1375 (*c*), on *Heracleum*, Forge Valley, Yorks, Oct. 1945.

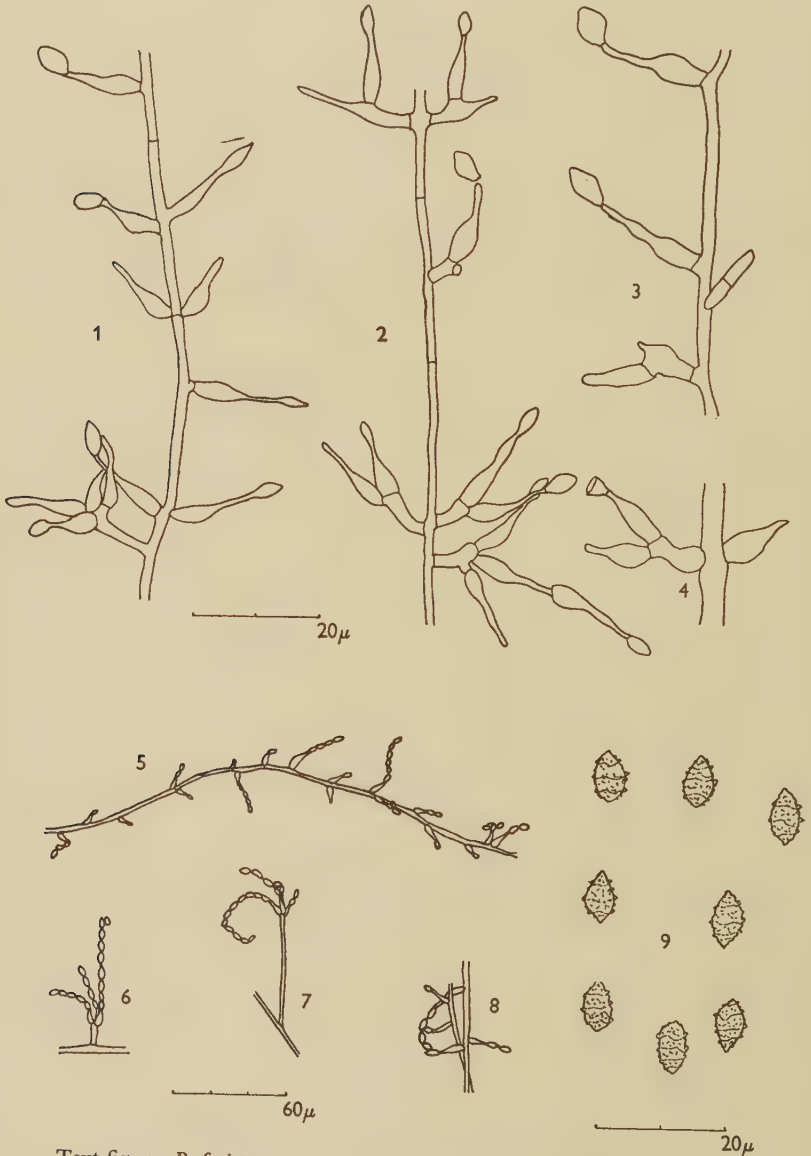
Although originally put apart from 'Taxonomic sp. I' in the C.M.I. folders, both the character of the colonies on the *Heracleum* stem and the size and shape of the conidia indicate identity with *P. herbarum*. The conidia are only slightly larger than in the other specimens, 9–11 × 4–5 μ, and this alone is considered to be insufficient ground for separation.

Paecilomyces fusisporus Saksena (1954), p. 187, pl. VIII, text-figs. 1–4 (Text-fig. 5)

The author's diagnosis runs as follows:

Colonies on Czapek's agar broadly spreading with medium rate of growth, completely occupying the Petri dish in 10 days at room temperature, slow growing, with superficial growth consisting mostly of trailing fertile hyphae, faintly zonate, surface white at first later becoming cream and slightly brownish; reverse of the same colour but more

brownish. Vegetative hyphae branched, hyaline, 3–4 μ thick, Fertile hyphae septate, branched, creeping. Conidial fructifications separate sterigmatic cells, or of verticils or series of verticils of branchlets and sterigmata irregularly distributed along the fertile hyphae; sterigmata 10–15 × 3–5 μ with pointed apices bearing conidia in long chains 100–125 μ; conidia fusiform with the two ends usually pointed, 6–10 × 3–5 μ, brownish in colour, walls thick showing characteristic spiral markings from end to end. The species is unmistakable on account of the markings on the spores.



Text-fig. 5. *P. fusisporus*. 1–4, conidial structures; 5–8, habit sketches of conidial structures; 9, conidia.

The following cultural data are based on our own findings.

Colonies on Czapek agar growing moderately well, spreading at first, becoming 25–30 mm. diam. in 7 days, but thereafter growing more slowly and never covering the surface of the agar in a Petri dish, white at first then quickly avellaneous, forming a close matted felt about 1 mm. thick, with fimbriate edge during the rapidly growing period, later with well-defined and much lobed margin; reverse pinkish brown.

Colonies on malt agar growing at about the same rate, and eventually restricted to a diameter of about 50 mm., with surface slightly browner than on Czapek, and with reverse almost black, or with pale brownish centre and remainder almost black. Other details as on Czapek.

Colonies on potato agar very similar to those on Czapek, growing at about the same rate, differing in the colour of the reverse, which is clay-coloured in the centre, with irregular patches of very dark brown at the edges.

Discussion

Saksena (1954, p. 186) says: 'The general structure of conidiophores agrees with the generic description of *Paecilomyces*. The shape of phialides is somewhat different. It resembles more the sterigma of a monoverticillate *Penicillium*, i.e. it is a cylindrical cell with an acute more or less tapering apex rather than having a narrowed long neck as is described typically for the genus *Paecilomyces*.'

In our experience the phialides are occasionally of the shape described, but usually are constricted somewhat at the base and taper at about half their length to long narrow tubes, i.e. they are entirely typical of *Paecilomyces*. Also the ornamentation of the spores is seldom in the form of a well-defined spiral band, as described and figured by Saksena, but most frequently takes the form of a fine reticulation all over the surface. However, the spores are quite distinct from those of any other species of the genus.

In other respects our findings agree with those of the author.

Material studied

Pa 64. Culture received from C.M.I., Oct. 1954, and originating from Saksena (I.M.I. 57442).

Paecilomyces elegans (Corda) Mason et Hughes *apud* Hughes (1951), p. 27 (Text-fig. 6)

Penicillium elegans Corda (1838), p. 18.
Hormodendrum elegans (Corda) Bonorden (1851), p. 77.
Spicaria elegans (Corda) Harz (1871), p. 138.
Spicaria elegans (Corda) Harz var. *sorghina* Sacc. (1886), *Sylloge*, **4**, p. 166.
Mariannaea elegans Arnaud (1952), p. 196.

Colonies on Czapek agar at 24° C. growing moderately rapidly, becoming 20–30 mm. diam. in 7 days and 35–50 mm. in 14 days, 2–3 mm. deep, consisting of a dense matted basal felt with floccose funiculose overgrowth, becoming strongly funiculose and sometimes producing loose, erect synnemata, thinning abruptly to a thin slimy margin, which is sometimes

lobed or irregular and bears isolated tufts of conidiophores, white at first, remaining white or turning yellowish, pinkish, or pale buff, but always becoming white again as conidium production reaches a maximum; drops tiny, colourless, sparse; odour nil; reverse whitish, then turning pinkish (in one strain crimson) or, more commonly, fairly deep brown or orange-

Text-fig. 6. *P. elegans.* 1–4, habit sketches of conidial structures; 5–7, conidial structures; 8, conidia.

brown, varying somewhat even with the same isolate in successive cultures; hyphae of the basal felt usually brownish; conidial structures mostly complex, loose or compact, but varying from simple monoverticillate heads to structures with up to seven successive whorls of phialides and side-branches borne along a main axis, often with the side-branches rebranched before producing phialides; conidiophores arising from the basal felt, from aerial hyphae, or from funicles, usually 75–150 μ long but occasionally up to 500 μ, tapering, up to 7 μ diam. at the base, diminishing to 2–4 μ (1·5–5 μ) and then dilating again at the apex to about 6 μ diam., usually smooth but occasionally finely roughened near the base, septate; branches very variable, occurring mixed with phialides, with up to six elements in a whorl, decreasing in length towards the apex of the fructification, thus giving the latter a pyramidal shape, the lower ones often rebranched, 6–45 μ long by 2–4 μ diam.; phialides in whorls of up to seven, flask-shaped, with basal portion almost cylindrical or swollen in the middle, tapering at just over half the length to a long narrow tube 0·5–1·5 μ diam., the whole 9–20 μ by 2–3 μ at the broadest part; conidia smooth, fusiform, hyaline, white in mass, 4–6 × 1·5–2·5 μ, adhering obliquely in the chains; conidial chains at first divergent, then bent and twisted and often tangled, up to 200 μ long, sometimes partially sliming down to form balls or irregular masses.

Colonies on malt agar similar in every way to those on Czapek, but strains which tend to produce incipient coremia do so more readily than on Czapek.

Colonies on potato agar growing slightly less rapidly than on Czapek, 17–25 mm. in 7 days and 35–60 mm. in 14 days at 24° C., otherwise similar.

Conidia swell before germinating, becoming almost globose and about 4·5 μ diam. Two successive germ-tubes are usually produced.

Growth at 8° C. is very slow, first becoming visible after about 10 days, and forming a colony only 1–2 mm. diam. in 3 weeks. Growth is still slow at 10–14° C., but good at 24–30° C., and nil at 37° C.

Discussion

Corda's illustration in *Icones* II leaves little doubt that he had a species of *Paecilomyces*. Bonorden's transfer of *Pen. elegans* to his new genus *Hormodendrum* was a complete misinterpretation of Corda's figure and description, as it is certainly not congeneric with *Cladosporium*, of which *Hormodendrum* is now considered to be a synonym. Harz (1871) transferred it to *Spicaria*, but without seeing any exsiccata, and, though it is quite possible that it is congeneric with *S. nivea* Harz, it is certainly not related to *S. solani* Harting, the type species of *Spicaria*.

Thom (1930) referred to *Pen. elegans* in the chapter on *Paecilomyces* but made no new combination, although Chesters (1948) included *P. elegans* (Corda)? Thom in a list of soil fungi. Hughes (1951) published a full description of the fungus, drawn both from fresh isolates and the type in Corda's herbarium, and made the new combination which now stands.

There is nothing in Saccardo's description of *S. elegans* var. *sorghina* to suggest any significant difference from *P. elegans* as here understood.

No material is available of *Mariannaea elegans* Arnaud, but the description, figure, and habitat, are sufficient to identify the fungus as *P. elegans*.

Occurrence

Corda's original isolate was from the inner surface of the bark on rotting pine trunks. It was recorded (as *Pen. elegans*) from rotten wood by Grove (1885), Massee (1893), and Hughes (1951). It has been reported from soil by Jensen (1912), Gilman & Abbot (1927), and Paine (1927).

Material studied

Pa 36. Culture from C.B.S., Nov. 1951, as *Spicaria elegans* (Cda.) Harz, C.B.S. isolate. Produces deep reddish brown colour in reverse, and abundant synnemata. Conidia sometimes slime down to form loose masses.

Pa 37. Culture from C.B.S., Nov. 1951, as *Spicaria elegans* (Cda.) Harz, C.B.S. isolate. Reverse of colonies in pale pinkish shades; abundant synnemata; little tendency for conidial chains to disintegrate.

Pa 52. Culture from C.M.I., Feb. 1952, as *P. elegans* (Corda) Mason et Hughes, I.M.I. 22573 (*a*), isolated in Feb. 1948 from *Betula* periderm, Richmond park, Surrey. Moderately deep brown in reverse of colonies; conidial chains often sliming down; produces very large and complex sporing structures but only very small synnemata.

Pa 53. Culture from C.M.I., Feb. 1952, as *P. elegans* (Corda) Mason et Hughes, I.M.I. 27616 (*a*), isolated in Apr. 1949 from conifer wood, Roche Abbey, Yorks. Only feebly pigmented in reverse of colonies; shows little tendency for conidial chains to become slimy.

Pa 23. Culture from J. H. Warcup, Dec. 1950, as *Paecilomyces* sp. K 2/1, from soil. Differs from the other strains examined in producing a crimson colour in reverse of colonies on agar. In view of the fact that Pa 37 tends to assume pinkish shades in reverse, and that in all other respects Pa 23 is indistinguishable from the other isolates, it has been considered inadvisable to regard this as a distinct species, or even variety.

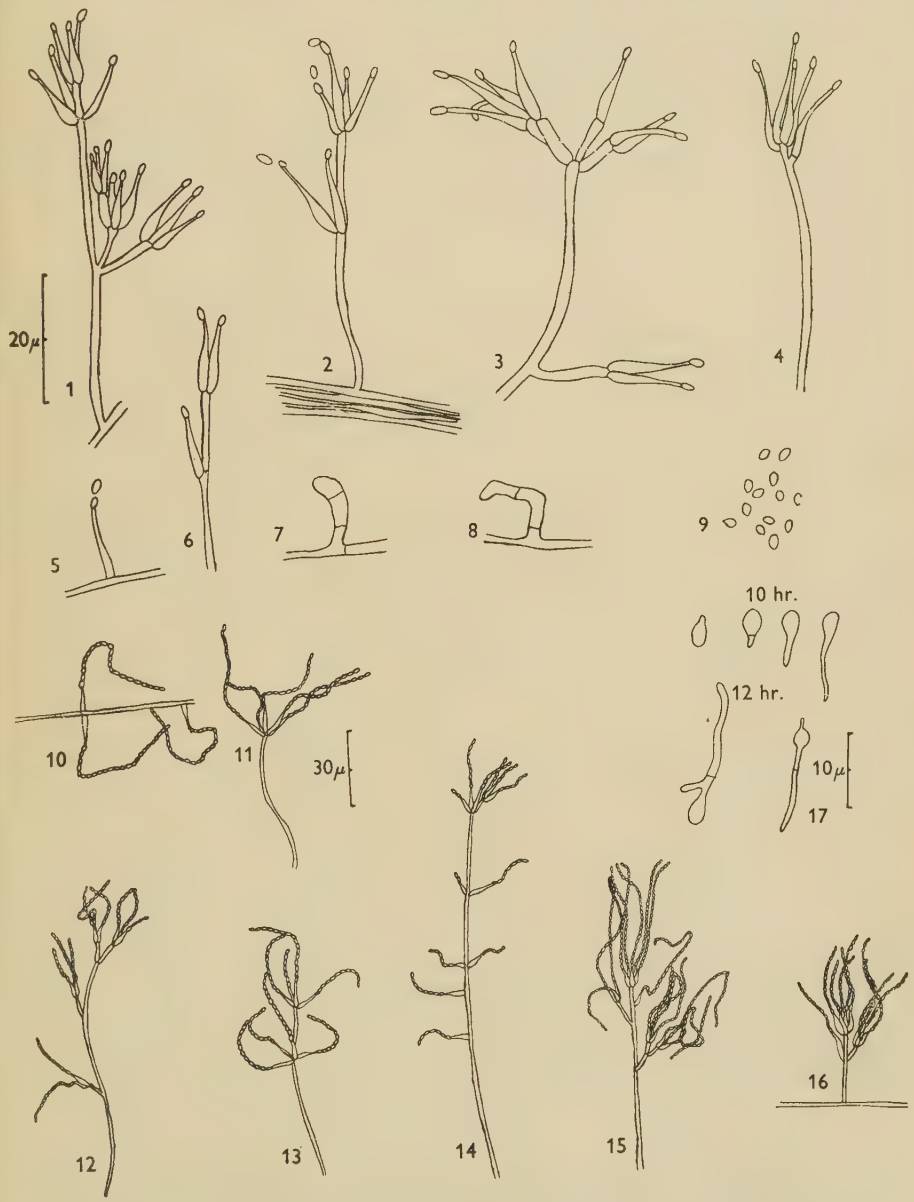
Pa 34. Isolated from the inner surface of bark of fallen pine tree, Dunkeld, Perthshire, Sept. 1953. Produces deep brown colour in reverse of colonies; synnemata small; conidial chains fairly persistent.

Paecilomyces farinosus (Dicks. ex Fr.) comb.nov. (Text-fig. 7).

(*Ramaria farinosa* Dickson (1790), p. 25.)
Isaria farinosa Fries, *Syst. mycol.* **3**, p. 271 (1832).
Spicaria farinosa Vuillemin (1911), p. 76.
Spicaria verticilloides Fron (1911), p. 483.
Spicaria farinosa verticilloides Fron (1912), p. 153.
Coremium swantoni A. L. Smith (1919), p. 156.
Spicaria aleyrodis Johnston (1917), p. 79.
Coremium breve Petch (1926), p. 259.
Coremium gracile Petch (1926), p. 260.
Spicaria (*Isaria*) *swantonii* (A. L. Sm.) Petch (1931), p. 103.
Spicaria gracilis Petch (1932*a*), p. 241; (1942), p. 261.
?*Paecilomyces subflavus* Szilvinyi (1940/41), p. 176.
There are probably many other synonyms.

Colonies on Czapek agar at 24° C. growing moderately well, 20–25 mm. in 7 days and 44–45 mm. in 14 days, varying in depth from 1·5 to 4 mm., consisting of a tough matted basal felt and a loose, hairy, floccose over-

growth, becoming more funiculose in age, with the basal felt usually yellowish and the overgrowth white or very faintly yellowish; drops nil; odour nil; reverse at first white, usually becoming pale bright yellow from centre outwards, occasionally pale orange, more or less zoned; sporing structures varying greatly in complexity, from single detached phialides to penicillate heads with several stages of branching; conidiophores normally



Text-fig. 7. *Paecilomyces farinosus*. 1–6, conidial structures; 7–8, abortive heads; 9, conidia; 10–16, habit sketches of conidial structures; 17, germinating conidia.

short and arising from the aerial hyphae, occasionally however from the basal felt and then longer, up to 300 μ by 0·8–2 μ diam., septate, smooth; phialides in whorls of up to 7, flask-shaped, with the typical slender terminal portion 0·5 μ or less in diam., 5–15 μ long and 0·8–2 μ diam. at broadest part; conidia broad elliptical or somewhat fusiform, smooth, 2–3 × 1–1·8 μ, in rather short chains (up to 90 μ) which are normally divergent or tangled but occasionally form irregular columns.

Colonies on malt agar similar except that the reverse colour is usually deeper, sometimes bright orange.

Colonies on potato agar similar to those on Czapek.

Most strains of this species tend to change somewhat on continued cultivation, becoming less pigmented in reverse and with simpler sporing structures. It is rare for true coremia, such as are found on insects, to be produced in culture, even in fresh isolates.

Conidia swell before germination to 3–3·5 × 2–2·5 μ and usually put out two successive germ-tubes.

Germination of conidia is very tardy at 8° C. and subsequent growth exceedingly slow. Growth is slow at 10–14° C., moderate at 24° C., slow at 30° C. and nil at 37° C.

Discussion

This fungus has been recorded frequently on various insects, usually as *Isaria farinosa*. A good summary of the literature is given by Petch (1934).

Vuillemin (1911) pointed out that the form genus *Isaria* includes a number of heterogeneous elements. He considers (rightly) that the method of conidium production is of much greater importance for classification than the presence or absence of coremia, and he therefore transferred *I. farinosa* to *Spicaria*. He was followed by Fron (1911), Picard (1914), Beauverie (1914) and Petch (1934). All the published descriptions indicate that the common insect parasite known as *I. farinosa* or *S. farinosa* is a true *Paecilomyces*.

The form described by Fron (1911) as *S. verticilloides*, altered later (1912) to *S. farinosa verticilloides*, has slightly larger conidia than most isolates, and somewhat deeper yellow colour in the mycelium. The differences do not warrant the retention of Fron's specific epithet.

The description of *S. aleyrodis* Johnston (1917) is very meagre, but the figures clearly indicate a *Paecilomyces*. From the lack of colour, size of spores, and its occurrence on *Aleyrodis variabilis*, it is obviously closely related to *P. farinosus* and is probably to be regarded as synonymous.

P. subflavus Szilvinyi is not identifiable with certainty in the absence of cultures, but is close to, and probably identical with, *P. farinosus*.

Spicaria swantonii (A.L.Sm.) Petch and *S. gracilis* Petch are undoubtedly *P. farinosus* (see below). *Coremium breve* Petch and *C. gracile* Petch are regarded by Petch (1932*a*) as synonymous with *S. gracilis*.

Material studied

Pa 46. Culture from C.B.S., Nov. 1951, as *S. verticillata* (Cda.) Lindau, received from Beckhuis v. Till. Colonies are fairly typical, but are somewhat lax in texture, and conidial heads are somewhat more complex than in most isolates.

Pa 49. Culture from C.B.S., Nov. 1951, as *S. farinosa* (Dicks.) Fr., received from E. W. Mason. This has probably deteriorated since isolation as it produces very little reverse pigment and the sporing structures are mostly very simple.

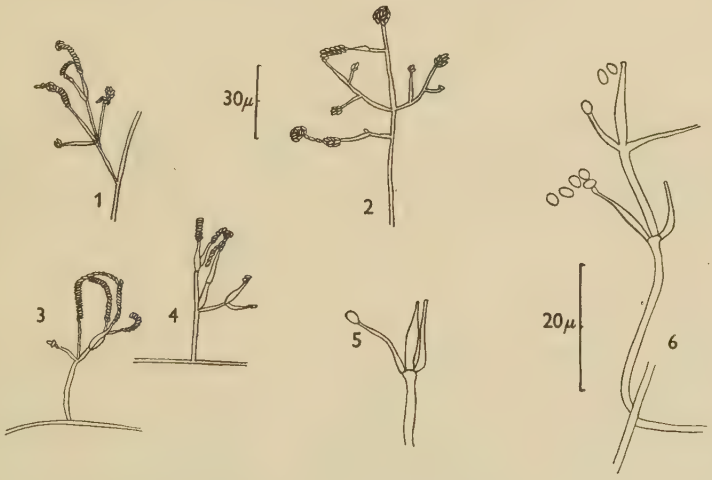
Pa 50. Culture from C.B.S., Nov. 1951, as *S. farinosa* (Dicks.) Fr., C.B.S. isolate. Typical in every way.

Pa 58. Culture from E. W. Mason, C.M.I., isolated from pupae of cabbage moth by A. E. Muskett, 1953. Produces good yellow colour, abundant sporing structures and loose coremia in old cultures.

Herb. Petch R. 920, R. 923, R. 927, labelled '*Spicaria swantonii*'; R. 380, R. 432, labelled '*Spicaria gracilis*'; about fifty specimens labelled '*Isaria farinosa*'. All the specimens, which were on a variety of insects, were similar as far as could be determined. Growth was white to pale cream, funiculose, and in many cases coremial. Specimens from which it was possible to make useful slides showed typical *Paecilomyces* conidial structures, with phialides ranging from 6 to 12 μ long and 1·5–2 μ diam. at widest part, tapering to a fine tube about 0·5 μ diam., and conidia 2–2·8 × 1–1·5 μ. There is little doubt that all the specimens represent *P. farinosus*.

Cordyceps militaris (Fr.) Link *stat. conid.* (Text-fig. 8).

Colonies on Czapek agar at 24° C. growing fairly rapidly, 20–23 mm. in 7 days and 40–45 mm. in 14 days, varying in depth from 2 mm. to the limits of the Petri dish, loose floccose, becoming denser in age, white tinged with yellow in the centre; drops nil; odour nil; reverse white with a central



Text-fig. 8. *Cordyceps militaris*. 1–4, habit sketches of conidial structures; 5–6, conidial structures.

spot of clear yellow; sporing structures simple, consisting of single phialides borne directly on aerial hyphae, or of loose branching systems which are seldom recognizably penicillate; conidiophores 30–45 μ long and 1–2 μ diam., slightly swollen at the apex, smooth, septate; phialides very variable, sometimes of the *Paecilomyces* type, sometimes tapering gradually from base to apex, 10–19 × 1–1·5 μ at widest part; conidia variable, subglobose elliptical or cylindrical, 2–3·2 × 1·5–2 μ, in short chains,

but with the spores lying broadside on to one another or more or less diagonally, or sliming down completely to form irregular spore balls.

Colonies on malt agar similar, but growing somewhat less rapidly; spores mostly slightly larger, 2·5–4 × 1·5–3 μ.

Colonies on potato agar similar to those on Czapek but somewhat less dense; spores mostly in irregular masses, rarely in chains.

Discussion

This species seems to form a link between *Paecilomyces* and *Cephalosporium*, since the phialides may be typical of either genus and the spores may be either in chains or in balls. In cultural characteristics it is very similar to *P. farinosus*. This similarity was noticed by Tulasne and by de Bary, who both considered *Isaria farinosa* to be the conidial state of *Cordyceps militaris*.

Petch (1934) discussed the question at length and also examined isolates of the conidial state of *C. militaris*. He states that his findings agree with those of E. W. Mason and concludes: 'The conidial stage of *Cordyceps militaris* is a *Cephalosporium*, which occurs on the mycelium on the larva or pupa bearing the *Cordyceps*. It has not been known to produce an *Isaria* form in nature or in culture'. He further states categorically that *I. farinosa* is not related in any way to *C. militaris*.

Petch stated that the conidia are sometimes produced in chains, so that his findings agree substantially with ours.

Material studied

In view of the frequent statements in the older literature that *I. farinosa* is the conidial state of *C. militaris*, is was deemed advisable to examine cultures made from ascospores of *C. militaris*. A specimen of the latter was collected at Virginia Water in September 1952, and a number of cultures were made from whole and part ascospores. So far as could be determined, these were all identical.

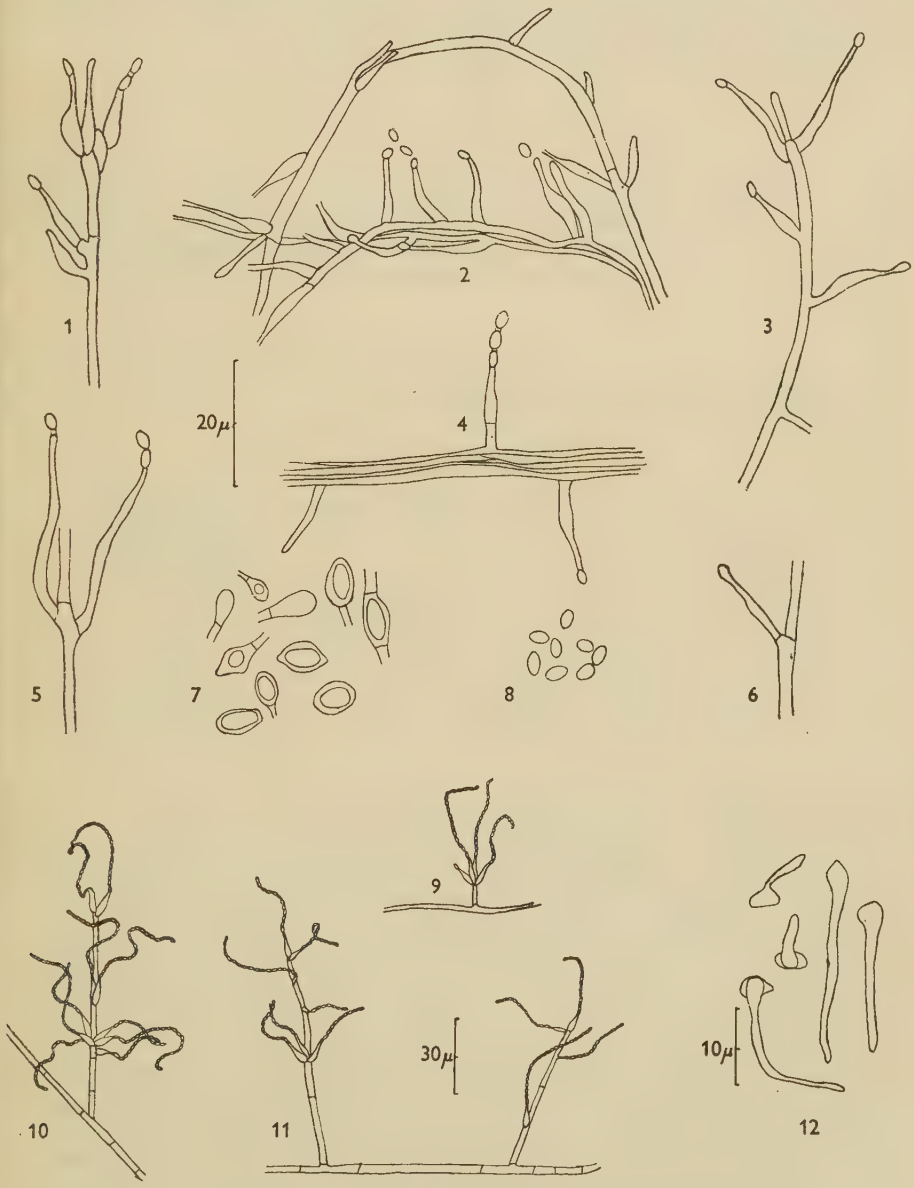
Paecilomyces puntonii (Vuill.) Nannizzi (1934), p. 245 (Text-fig. 9).

Corethropsis puntonii Vuillemin (1930), p. 1334.

Colonies on Czapek agar at 24° C. growing rapidly, attaining a diameter of 45–70 mm. in 7 days and covering a dish in 14 days, up to 2 mm. deep, matted funiculose, with margin of regular outline in the early stages, eventually tending to climb up the sides of the culture vessel, white, becoming dirty white or tinged with yellow in patches; exudate lacking or limited to a few large colourless drops in age; odour nil or faintly mouldy; reverse white to dirty white or pale greyish buff to somewhat greenish, particularly in the centre; conidial structures variable but always fairly simple, consisting of phialides scattered along aerial hyphae or funicles, singly or in small groups, or forming small verticils on lateral branches; conidiophores often lacking, when present mostly short to very short, 6–24 × 1·5–2·5 μ, smooth, septate; phialides 10–16 μ long, with cylindrical basal portion 1·5–2·5 μ diam., tapering gradually to a long thin tube only about 0·5 μ diam.; conidia cylindrical to fusiform, smooth, 3–5 × 1·5–2 μ (average 3·7 × 1·9 μ), in chains up to about 100 μ long, straight or sinuous,

seldom tangled; macrospores usually abundant, terminal or intercalary, subglobose to irregular, 4–8 × 4–6 μ.

Colonies on malt agar spreading more rapidly than on Czapek, 40–50 mm. diam. in 4 days and covering the dish in 7–8 days, with colour and texture as on Czapek; reverse orange-buff to pale dull brown; sporing structures as on Czapek, including abundant macrospores.



Text-fig. 9. *P. puntonii.* 1–6, conidial structures; 7, macrospores; 8, conidia; 9–11, habit sketches of conidial structures; 12, germinating conidia.

Colonies on potato agar growing slightly more rapidly than on Czapek, 32–50 mm. in 4 days and 70–90 mm. in 7 days, with colour and texture as on Czapek; reverse dull orange-yellow to dull brown; sporing structures as on Czapek except that there is usually more variation in size of macrospores, 4–13 × 3–5 μ.

Conidia swell to 4 × 3 μ before germinating, then put out a single polar germ-tube; very occasionally a second, lateral, germ-tube appears later.

This species does not grow at 8°, grows very slowly at 10–14°, spreads rapidly at 24° and even more rapidly at 30–37° C.

Discussion

The mould was first described by Vuillemin (1930) as *Corethropsis puntonii*, having been isolated by Puntoni from human skin. Nannizzi (1934) transferred it to *Paecilomyces*. Baldacci (1938) published an extensive study of the mould, starting with a subculture from Puntoni's original isolate. Our findings agree in all essentials with his.

Occurrence

The four isolates studied are from different sources. Hence this species is probably widespread but not common.

Material studied

Pa. 2. Culture from C.B.S., Nov. 1950, as *Paecilomyces puntonii* (Vuill.) Nann., ex Ciferri. Agrees well with Nannizzi's and Baldacci's descriptions but produces few conidia.

Pa 10. (=Ad 195.) Received (at Ardeer) from A.T.C.C., Nov. 1927, as *Paecilomyces* sp. no. 1138. Produces few conidia but is otherwise typical.

Pa 15. (=B.B. 123.) Culture from B.C.I.R.A., July 1930, as *Paecilomyces* sp. This is quite typical and still produces abundant conidia.

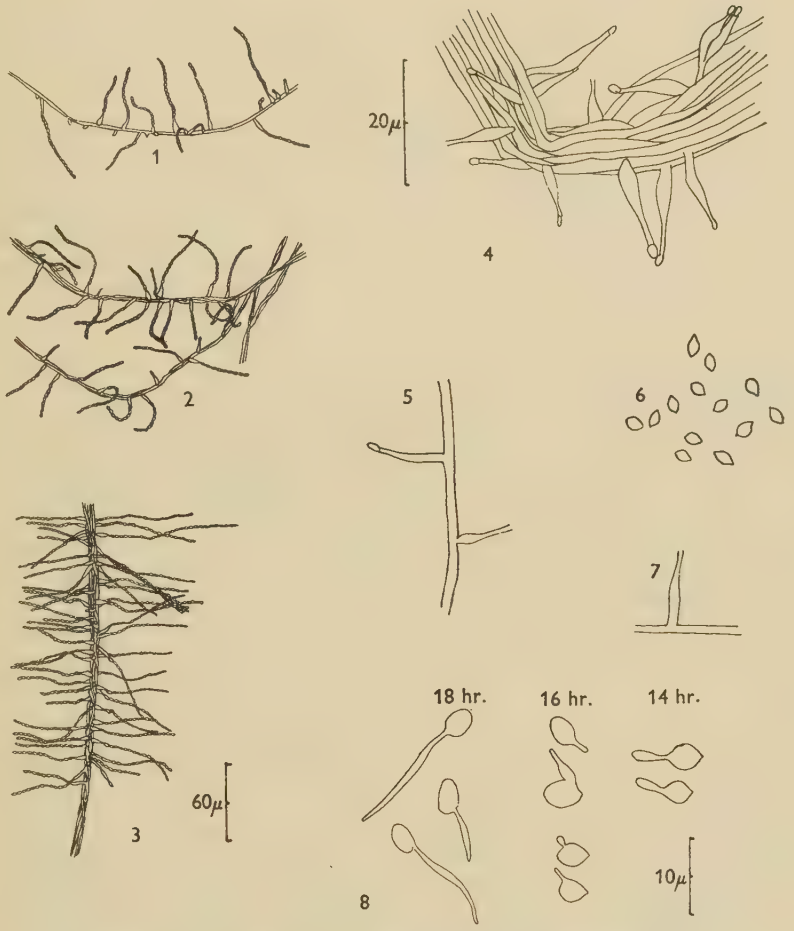
Pa 68. Culture from Dr B. H. Howard, Rowett Research Institute, Aberdeen, received Jan. 1956 as *Sporotrichum* sp.? isolated from mouldy silage. Quite typical, producing abundant conidia and macrospores.

Paecilomyces flavescens sp.nov. (Pl. 2, fig. 3; Text-fig. 10)

Coloniae in agaro Czapekii modice crescentes, ad 2 mm. in altitudinem, floccosae et funiculosae, albae dein pallidae flavidae aut cum margine flavida et medio albido-roseo, guttulis parvissimis et reverso albido dein albido-flavido. Coloniae in decocto tuberorum cum agaro aliquantum flaviores et funiculosiorae. Conidiophora absentia; phialides in hyphis aetheriis aut funiculis hypharum incompositae, 9–15 μ long., basi 1·8–2·5 μ diam. et ultima parte longa, 0·5–1 μ diam.; conidia ovata aut fusiforma, levia aut asperula, 3·5–4 × 2–2·6 (2·8) μ, in catenis rectis aut undatis sed nunquam intricatis, ad 60 μ longis. Fungus in solo, Ampthill Forest Nursery, Angliae, per Mrs Brind inventus.

Colonies on Czapek agar at 24° C. growing moderately well, 13–15 mm. in 7 days and 30–36 mm. in 14 days, about 2 mm. deep, floccose funiculose with regular margin, white then tinged with yellow, or with margin yellowish and centre faintly pink; a few very small drops produced in age; odour nil; reverse white then faint yellow; conidiophores entirely lacking, sporing structures consisting of very numerous phialides borne irregularly on aerial hyphae or funicles; phialides elongated flask-shaped, 9–15 μ long,

with basal portion 1·8–2·5 μ diam., tapering to a long tube only 0·5–1 μ diam.; conidia short oval or fusiform, smooth or finely roughened, 3·5–4 × 2–2·6 (2·8) μ, borne in short chains, up to 60 μ long, which are straight or slightly undulate but never tangled.



Text-fig. 10. *P. flavescens*. 1–3, habit sketches of conidial structures; 4, 5, 7, conidial structures; 6, conidia; 8, germinating conidia.

Colonies on malt agar somewhat more restricted than on Czapek, 13–17 mm. in 7 days and 27–30 mm. in 14 days, usually becoming pale yellow in sectors or patches; occasional very short conidiophores produced, usually bearing two phialides; other details as on Czapek.

Colonies on potato agar usually somewhat yellower than on Czapek and more markedly funiculose, otherwise similar.

This species is characterized by its production in colonies of patches of clear pale yellow, by its lack of penicillate sporing structures, and by its very funiculose habit. In mature colonies the hyphal ropes are thickly

covered with perpendicular phialides bearing their almost straight conidial chains.

Conidia swell to about $5 \times 3{\cdot}5\,\mu$ before germination, but mostly retain their characteristic shape, then put out two successive germ-tubes and occasionally a third.

There is barely visible evidence of growth after 14 days' incubation at 8° C. Growth is very slow at 10–14° C., moderately good at 24° C., somewhat better at 30° C. and very slow at 37° C.

Material studied

Pa 35. The only isolate available for study, received as a culture from C.M.I., Kew, and sent to them by Mrs Brind. Isolated from Ampthill Forest Nursery soil.

Herb. I.M.I. no. 45948, labelled '*Paecilomyces* species'. Consisted of three dried cultures of the same isolate as Pa 35, one on potato-carrot-agar and two on Dox plus yeast medium. General appearance and measurements agreed with the findings recorded above.

Paecilomyces parvus sp.nov. (Pl. 2, fig. 4; Text-fig. 11)

Coloniae in agaro Czapekii lentissime crescentes, tenuissimae, humidae, hyalinae aut albidae, margine inaequali et reverso hyalino, conidia tardissime gerentes aut nulla. Coloniae in agaro 'malt' dicto primo humidae tarde funiculosae, albidae aut bubalinae dein cum maculis albido-roseis, reverso bubalino; conidia primo rara, subcopiosa tribus post mensibus. Coloniae in decocto tuberorum cum agaro humidae dein funiculosae, albidae, reverso primo albido dein bubalino, albido-roseo, aut albido-aurantiaco, conidia tribus post hebdomadibus gerentes. Conidiophora ad 30μ long. et $1{\cdot}5$–2μ diam., levia, septata, saepe cum apice aliquantulum dilato; penicilli plerumque monoverticillati, cum phialidibus perpaucis; phialides 5–11 μ long., basi $1{\cdot}2$–$2\,\mu$ diam. et ultima parte longa, $0{\cdot}5\,\mu$ diam.; conidia subglobosa aut elliptica, levia, $2{\cdot}5$–$3 \times 1{\cdot}5$–$2{\cdot}4\,\mu$, in catenis brevibus intricatis.

Cultus ex C.B.S., Baarn, *Paecilomyces burci* (Poll.) Thom appellatus sed ad hunc non pertinet.

Colonies on Czapek agar at 24° C. growing very slowly, 7–9 mm. in 7 days and 21–23 mm. in 15 days, very thin, moist, colourless to whitish, with margin ill-defined and irregular; reverse colourless; sporing very tardily or not at all.

Colonies on malt agar growing at same rate as on Czapek, consisting at first of a wet basal felt with small funiculose tufts 0·5–1 mm. high, with the tufts gradually extending, and finally the whole colony becoming funiculose, with margin more or less regular and circular, very pale buff to white, becoming tinged with pink and yellowish buff; odour nil; drops nil; reverse pale buff, becoming dirty brown in centre; sporing structures sparse at first but fairly abundant after 3 months.

Colonies on potato agar growing at same rate as on Czapek, first forming a thin wet felt, then gradually developing funiculose aerial mycelium about 1 mm. deep, white to cream; odour nil or faintly alcoholic; drops nil; reverse dirty white at first then very pale buff, faint pink or faint orange; sporing structures produced fairly freely after about 3 weeks' incubation; sporing heads mostly monoverticillate with very few phialides; conidiophores arising from funiculose aerial hyphae, up to $30\,\mu$ long and $1{\cdot}5$–$2\,\mu$ diam., smooth, septate, often slightly swollen at tip; phialides swollen at

the base, tapering at just over half the length to a long thin tube about 0·5 μ diam., 5–11 μ by 1·2–2 μ diam. at the broadest part; conidia subglobose to elliptical, smooth, 2·5–3 × 1·5–2·4 μ, in short chains which become intricately tangled.

Text-fig. 11. *P. parvus*. 1–5 and 7, conidial structures; 6, conidia; 8, germinating conidia; 9–11, habit sketches of conidial structures.

On corn meal agar growth is slow but sporing structures are produced fairly abundantly.

Conidia swell before germination to about 4 × 3 μ, then put forth a single polar germ-tube. Very occasionally a second germ-tube is produced laterally.

Growth is very slow at 8° C. but eventually colonies spread widely and produce conidia, it is similar at 10–14° C., slow at 24° C. and nil at 30–37° C.

Material studied

Pa 3. Culture received from the C.B.S., Baarn, as *Paecilomyces burci* (Poll.) Thom, received by them from Stühmer. It does not correspond with Pollacci's description or with Thom's amended diagnosis, growing more slowly than *P. burci* and having smaller conidia. In addition, *P. burci* was isolated by Pollacci from a tumour in a woman, and it is most unlikely that a mould incapable of growing even at 30° C. would be found in such a situation. Since this isolate does not fit with any of the other species of *Paecilomyces* described here, it is to be regarded as a new species.

Section *Floccosi*

Paecilomyces victoriae (Szilvinyi) comb.nov. (Text-fig. 12)

Penicillium (*Paecilomyces*) *victoriae* Szilvinyi (1936), p. 535.

Colonies on Czapek agar at 24° C. growing moderately well, 27–30 mm. in 7 days and 45–50 mm. in 14 days, loosely floccose, thickest in the centre and thinning towards the margin, becoming very slightly funiculose, in age dying down, with narrow submerged margin, at first regular then becoming lobed, white at first then becoming zoned with faint greyish green; drops nil; odour nil; reverse white becoming indistinctly zoned with pale yellowish buff; sporing structures usually fairly compact, asymmetric, mostly with a single verticil of metula-like branches, or of branches and phialides mixed, more rarely with two or more stages of branching below the phialides; conidiophores arising from aerial hyphae, 30–90 × 1·4–1·7 μ, smooth, septate, often slightly dilated at the tip; phialides up to 5 in a whorl, 9–19 μ long, with almost cylindrical base 1–1·8 μ diam. tapering fairly abruptly at just over half the length to a slender tube about 0·5 μ diam.; conidia ellipsoid to subglobose with one end bluntly pointed, smooth, 2·2–3·1 × 1·4–2 μ, mostly 3 × 2 μ, in chains which are either loosely tangled or in loose columns up to 60 μ long.

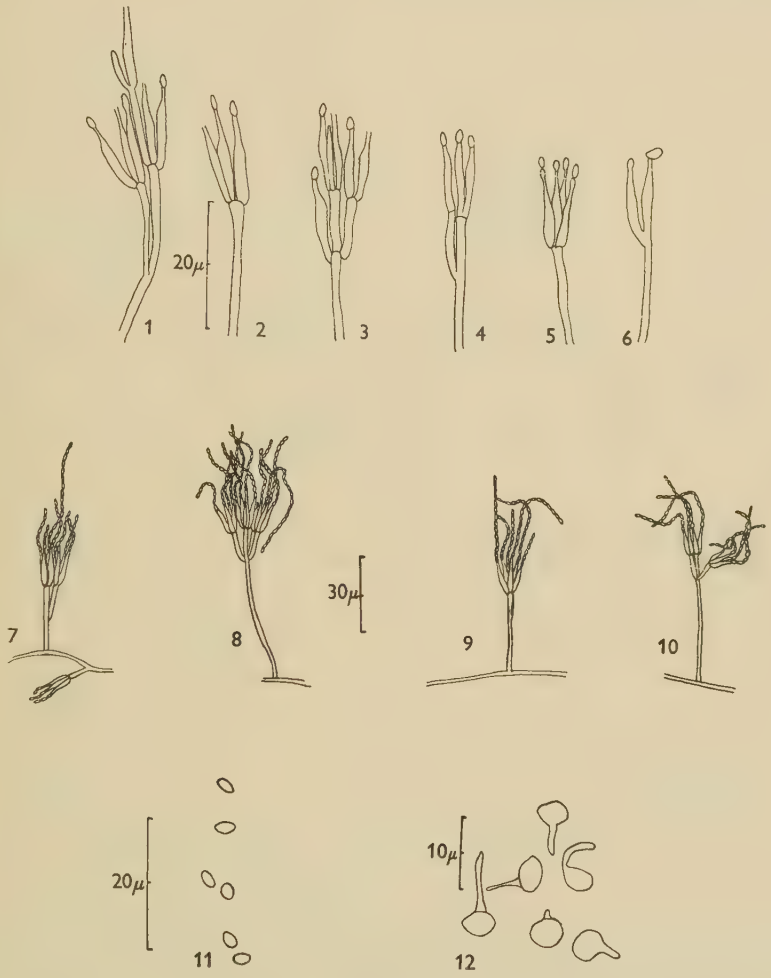
Colonies on malt agar growing slightly more quickly than on Czapek, 34–36 mm. in 7 days and 55–60 mm. in 14 days, very similar to colonies on Czapek but usually with a suggestion of pink in the somewhat funiculose margin in age; reverse deep brown in the centre shading to pale orange at the margin, with long radial cracks in the agar; heads comparatively simple, with two to three branches bearing phialides or with a whorl of phialides only, often reduced to single phialides borne directly on aerial hyphae; phialides and conidia as on Czapek.

Colonies on potato agar growing more rapidly than on Czapek, 38–39 mm. in 7 days and almost covering the dish in 14 days usually with a pinkish sheen spreading over the whole surface in age, and with numerous, tiny, pinkish drops; otherwise as on Czapek.

The first few subcultures from the culture received from Baarn (see below) produced a pinkish colour in reverse and occasionally a central red zone. On plates with numerous colonies (the first few of a dilution series) incubation in the light gives grey-green colonies, in the dark pink to vinaceous colonies with only traces of a greenish tint.

Conidia swell and become almost globose before germination, then produce successively two or three germ-tubes.

The fungus does not grow at 8° C.; growth at 10–14° C. is very restricted, at 24° C. moderately rapid and more rapid at 30–37° C., with an optimum probably between 30° and 37° C.



Text-fig. 12. *P. victoriae.* 1–6, conidial structures; 7–10, habit sketches of conidial structures; 11, conidia; 12, germinating conidia.

Isolated by Szilvinyi from tobacco from Sumatra. The author recognized that his species belongs in *Paecilomyces* but he regards the latter as merely a section of *Penicillium*. Hence the necessity for a transfer to *Paecilomyces*.

Material studied

Pa 5. Culture from C.B.S., Nov. 1950, as *Paecilomyces victoriae*. Szilvinyi. It was received from von Szilvinyi and is probably the type strain.

Paecilomyces marquandii (Massee) Hughes (1951), p. 30, fig. 7 (Text-fig. 13)

Verticillium marquandii Massee (1898), p. 24.
Spicaria violacea Abbott (1926), p. 26, fig. 3.
Spicaria violacea Petch (1932), p. 239, fig. 5*d*.

Colonies on Czapek agar at 24° C. growing moderately well, 18–25 mm. in 7 days and 36–45 mm. in 14 days, floccose 2–3 mm. deep, becoming somewhat funiculose only in age, sometimes radially wrinkled, sometimes,

Text-fig. 13. *P. marquandii*. 1–2, habit sketches of conidial structures; 3–8, conidial structures; 9, conidia.

particularly when freshly isolated, producing finger-like coremia about 1 cm. long, white at first rapidly becoming violet, or occasionally somewhat redder shades; drops very small and colourless or lacking; reverse rapidly bright yellow, becoming orange-yellow or brownish yellow, with the colour diffusing into the agar; conidial structures varying in complexity from isolated phialides to penicillate structures with a main axis bearing a terminal whorl of phialides and further whorls of phialides and branches from lower nodes, but with isolated phialides infrequent and mono-verticillate heads common; conidiophores arising from aerial hyphae, 15–90 μ long, or more rarely from the surface of the medium and then up to 300 μ long, at the base 2·6–3 μ diam., tapering to a diameter of 1·5–2·4 μ and swelling again at the extreme tip to 3–3·5 μ, smooth, septate; branches

sometimes rebranching before bearing phialides, with the prophialides (metulae) fairly regular, 6–12 × 1·2–2·5 μ; phialides up to 6 in a whorl, flask-shaped, 8–15 μ long, with basal portion 1·5–2 μ diam., tapering gradually or abruptly at just over half the length to a slender tube 0·5 μ diam.; conidia broadly ellipsoid, usually showing a small connective at each end, smooth or occasionally very faintly roughened, 3–3·5 × 2–2·2 μ, in chains which are straight and divergent at first, then becoming entwined, 45–90 μ long.

Colonies on malt agar as on Czapek agar except that under very moist conditions there is a tendency to become slimy, and that there is less pigment in reverse.

Colonies on potato agar tending to become somewhat more funiculose, otherwise similar.

On all media some strains, when freshly isolated, produce coremia. On continued cultivation the faculty of forming coremia is gradually lost, and spore production tends to decline.

On germination conidia usually produce two successive germ-tubes.

There is no growth at 8° C., very slow growth at 10–14° C. (1 mm. in 7 days and 13–14 mm. in 14 days), moderate growth at 24° C., and somewhat slower growth at 30° C. There is no growth at 37° C. and after 3 weeks at this temperature the inocula are non-viable at 24° C.

Discussion

The fungus was first described by Massee (1898) as a *Verticillium* and stated to be common on the gills of *Hygrophorus virgineus* in Guernsey.

Abbott (1926*a*, *b*) isolated from soil a mould which he named *Spicaria violacea*. This was included by Raper & Thom (1949), in the Divaricata section of *Penicillium*, but without change of name. It was pointed out that *S. violacea* is closely related to *Pen. lilacinum* Thom, and is connected to the latter by intergrading strains.

Petch (1932), apparently unaware of Abbott's publication, described *S. violacea* Petch, from a Tineid case. As far as can be ascertained from his description and exsiccata his fungus was a strain of *P. marquandii*.

Hughes (1951) reports receiving from W. G. Bramley an isolate labelled *Verticillium marquandii* Massee. It was collected by K. G. Payne on the gills of *Hygrophorus virgineus*. Hughes compared this with one of the original collections of *V. marquandii* in Herb. Kew., ex Marquand in Guernsey, 10 September 1897, and found good agreement. However, it proved to be wrongly placed in *Verticillium* and was redescribed by Hughes as *P. marquandii*.

In the present study a subculture from Hughes's strain was grown side by side with *S. violacea*, Abbott's type strain. The two are practically indistinguishable and undoubtedly conspecific.

Material studied

Pa 21. Culture from N.R.R.L. (no. 901) as Abbott's type strain of *Spicaria violacea*. Isolated from soil. Produces deeply floccose colonies with the typical deep yellow reverse, but spores tardily and hence shows the characteristic violet colour somewhat belatedly.

Pa 28. Culture from J. H. Warcup, 1949. Isolated from soil, Lakenheath Warren, Suffolk. Spores tardily but eventually produces typical colonies.

Pa 48. Culture from C.B.S., Nov. 1951, as *Isaria* (*Spicaria*) sp., isolated by Prof. van Holder, Ghent, from soil. Strongly coloured and, when first received, produced numerous coremia.

Pa 54. Culture from C.M.I., Kew, as *Paecilomyces marquandii* (Massee) Hughes, I.M.I. 33204. Produces deeply floccose colonies, typically coloured.

Pa 55. Isolated from soil at L.S.H.T.M. by Mrs S. Marcus. Produced coremia when first isolated. Colonies deep violet, with abundant sporing structures.

Pa 61. Culture from C. T. Ingold, Birkbeck College, as *P. marquandii*, isolated from the gills of *Hygrophorus virgineus*, Oct. 1953. Colonies deeply floccose, typically coloured.

Herb. Petch R. 363, labelled '*S. violacea*, on a Tineid case, Newara Eliya, 3–12–1927'. A very tiny specimen covered with a funiculose, pink to buff mould. A preparation showed erect conidiophores with compact penicillate heads; phialides of the typical *Paecilomyces* shape, 7–11 × 1·5–2·5 μ; conidia broadly ellipsoid, smooth, with suggestion of connectives, 2–3 × 1·4–2 μ. There is little doubt that the mould is *P. marquandii*.

Penicillium lilacinum Thom (1910), p. 73, fig. 30

Spicaria rubido-purpurea Aoki (1941), p. 440.

This species, although it is not included in *Paecilomyces*, is mentioned here because of its close relationship to *P. marquandii*. Typical isolates of the two species are rapidly distinguished by colony characteristics. *P. marquandii* is pale greyish violet or lavender on the surface and citron yellow to orange yellow in reverse, whilst *Pen. lilacinum* is greyish vinaceous (more reddish than *P. marquandii*) on the surface and crimson to purple in reverse. In addition, the conidial structures of *P. marquandii* are definitely of the *Paecilomyces* type, whereas in *Pen. lilacinum* some phialides are more or less of the same type, but these are the exception and the majority are shorter and more abruptly pointed. The conidia of *P. marquandii* are ellipsoidal with pointed ends, 3–3·5 × 2–2·5 μ, usually slightly rough, those of *Pen. lilacinum* less markedly ellipsoidal, smooth, 2·5–3 × 2 μ.

However, as Raper & Thom (1949) have pointed out, intergrading forms are not uncommon. On the other hand, they state that *Pen. lilacinum* shows kinship with *Pen. janthinellum* Biourge, through a series of transition forms. It has, therefore, been considered best to leave *Pen. lilacinum* in the genus *Penicillium*.

Material studied

Pa 20. Culture from G. E. Turfitt, Nov. 1944, as an unidentified mould from soil. This shows some similarities to species of *Paecilomyces* but is best regarded as a strain of *Pen. lilacinum*. It spores very tardily, hence remains white for a long time. The reverse of colonies is strongly crimson, and the colour does not diffuse into the agar. Sporing structures are predominantly simple.

Pa 32. Culture from A. L. James, Timber Research Laboratory, Johannesburg, Nov. 1947, as T.R.L. 831. Spores somewhat tardily and becomes only very pale violet on the surface. Conidial structures are mostly simple.

Pa 47. Culture from C.B.S., Nov. 1951, as *Spicaria rubido-purpurea* Aoki, obtained from Kominami. This is a transition form, with a tendency to form a wet growth at first, becoming slowly floccose and finally funiculose, with reverse dull pink, with sometimes faint yellow in isolated spots. Complex sporing structures predominate.

N.R.R.L. 895. Culture received from K. B. Raper, July 1948, as the type strain of *Pen. lilacinum* Thom

A number of other strains of *Pen. lilacinum* in the L.S.H.T.M. collection appeared to be quite typical and were not examined in detail.

Paecilomyces javanicus (Friederichs et Bally) comb.nov. (Text-fig. 14)

Spicaria javanica Fried. et Bally (1923), p. 146, Pl. III.

Colonies on Czapek agar at 24° C. growing moderately well, 25–30 mm. in 7 days, and 47–68 mm. in 14 days, 2–4 mm. deep, forming at first a loosely floccose cushion, becoming more densely matted and eventually funiculose, with margin abrupt or gradually thinning, white at first becoming very pale blue-grey; drops nil in young cultures but numerous, colourless, tiny in age; odour nil or faint and sweet; reverse white at first, rapidly becoming clear pale yellow or yellow with patches of greenish yellow, finally zoned with greyish violet to blue-grey; conidial structures varying from single phialides to heads with a terminal whorl of phialides and with a few branches and phialides from lower nodes; conidiophores arising from aerial hyphae, 15–45 μ long, or from the mycelium close to the substrate and then longer, up to 400 μ, smooth, septate, 0·7–2 μ diam.; phialides in whorls of up to 5, (6) 9–11 (15) μ long, with almost cylindrical basal portion, 1·2–2 μ diam., and long tip 0·5–0·7 μ diam.; conidia cylindrical to fusiform, 4–6 × 1–1·5 μ, in long, almost straight chains, which seldom become tangled; abortive heads common, especially in slide cultures, consisting of swollen, curled and twisted hyphae in place of normal phialides.

Colonies on malt agar growing at same rate as on Czapek, differing only in producing less colour in reverse and in greater variation in size of conidia, 3·5–7 × 1–1·8 μ.

Colonies on potato agar growing at same rate as on Czapek, white, often tinged with yellow or pale grey in age; reverse white, developing a faint yellow or dull violet spot in the centre. Other details as on Czapek except that the conidia show more variation, 4–7 × 1–1·9 μ.

This species shows considerable variation in size of conidia, which vary also to some extent with the type of substrate.

Conidia swell and usually elongate before germination, then put forth two, sometimes three, successive germ-tubes, almost always polar.

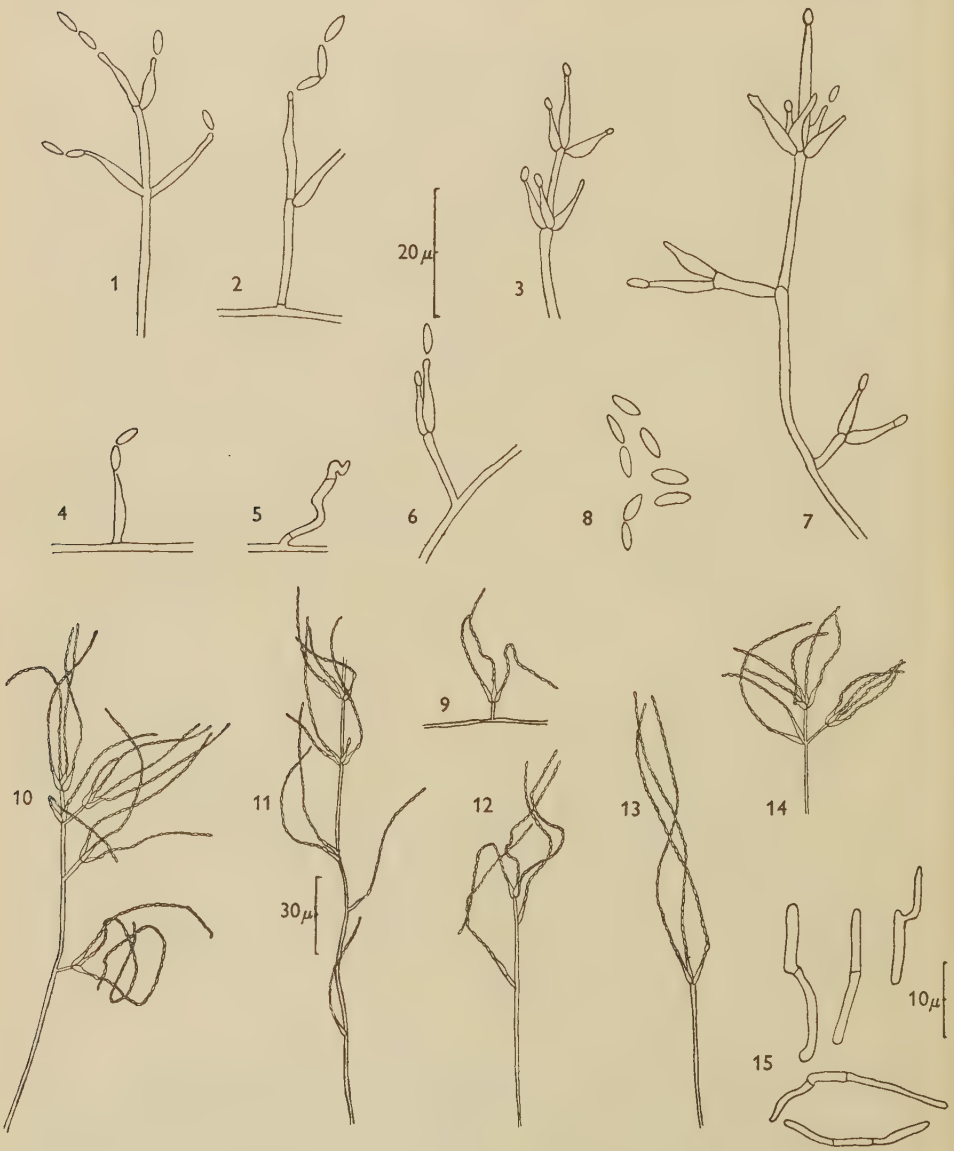
Growth is nil at 8° C., very slow at 10–14° C., normal at 24° C., restricted at 30° C., and nil at 37° C.

Discussion

The original English summary of the description by Friederichs & Bally (corrected for spelling) is as follows: 'Hyphae septate with septa, fertile hyphae richly branched, 1 or 2 μ broad. On the top numerous verticillate branchlets are formed. These primary branchlets form on their tip 3 to 4 secondary branchlets, on which rise the conidia in long chains. Conidia elliptical 2 × 1–1½ μ, first white, later grey-violet.'

The culture on which our own diagnosis is chiefly based was obtained from the C.B.S., who received it from Bally. It may be taken to represent

Bally's conception of the species. As will be seen by a comparison of our description with Friederich & Bally's, the latter's measurements of conidia do not agree with ours. This may be due to the fact that the size of the



Text-fig. 14. *P. javanicus*. 1–4, 6–7, conidial structures; 5, abortive head; 8, conidia; 9–14, habit sketches of conidial structures; 15, germinating conidia.

conidia varies with the substratum, or may possibly be due to a genuine error in measurement. Be that as it may we propose to regard the culture from Bally as representative of the species.

Petch (1925*a*) described a fungus from Ceylon as *Spicaria javanica* Bally. It was parasitic on species of *Ceroplastis*, and usually associated with *Cephalosporium lecanii*. Petch's cultural data include: basidia (i.e. phialides) 4–6 × 2–2·5 μ; branches single or in whorls of 2–6, bearing 1–6 basidia, and in some cases the basidia borne in whorls directly from the main stem of the conidiophore; spores in chains, narrow oval, with ends rounded or subacute, 3–4 × 1·2–1·5μ. Colony colour violet-grey; reverse yellow to deep orange.

Two specimens in Petch's herbarium were examined and were found to be similar. The fungal growth was white to faint yellow, and a typical specimen from which a satisfactory slide was prepared gave measurements agreeing substantially with those of Petch. The violet-grey colour mentioned in the diagnosis is, according to Petch, produced in culture but only tardily on insects.

Material studied

Pa 41. Culture from C.B.S., Nov. 1951, obtained from M. B. Schwartz. Produces only a faint violet colour and spores tardily and sparsely. Agrees, however, sufficiently well with Pa 42 to be regarded as the same species.

Pa 42. Culture from C.B.S., Nov. 1951, obtained from Bally. Regarded as typical of the species.

Herb. Petch R 174, labelled '*S. javanica* on caterpillars in lab., Nuwara Eliya, 31–5–27'. Consisted of a number of hairy caterpillars covered with funiculose growth up to about 2 mm. deep, white to yellowish; funicles with numerous lateral short conidiophores; heads large and complex, with tiny phialides densely packed; branches short, 3–4 in a whorl, often with secondary and tertiary branches; phialides with swollen base and long slender tip, 4–7 × 2 μ; conidia cylindrical to fusiform, 3–4 × 1·2–1·8 μ.

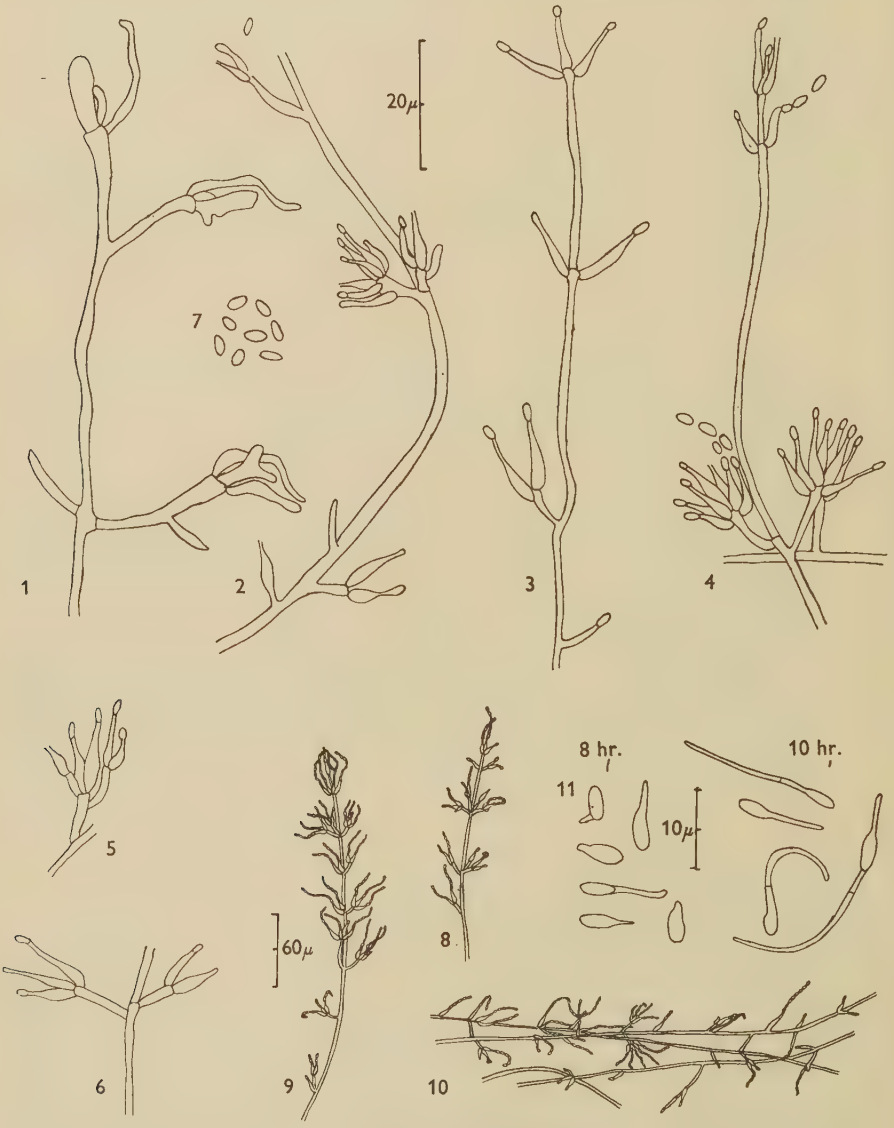
Unless *P. javanicus*, as it occurs on insects, forms spore heads which are very different from those produced in culture, this specimen is not representative of the species. Taken in conjunction with Petch's cultural data (above), our findings suggest possibly *P. marquandii*. Herb. Petch (no number), labelled '*S. javanica* Bally on *Euproctis flava*, Peradeniya, Jan. 1924'. This is very similar to R 174 in all respects and is undoubtedly the same species.

Paecilomyces fumoso-roseus (Wize) comb.nov. (Text-fig. 15)

Isaria fumoso-rosea Wize (1904), p. 721, fig. 7.
Spicaria aphodii Vuillemin (1911), p. 76.
Spicaria fumoso-rosea (Wize) Vassiljevski (1929), p. 146.
Paecilomyces hibernicus Kennelly et Grimes (1930), p. 513.

Colonies on Czapek agar at 24° C. growing moderately rapidly, 25–30 mm. in 7 days and 50–65 mm. in 14 days, deeply floccose, up to 5 mm. deep after 7 days and often touching the lid of the Petri dish after 14 days, later collapsing and becoming somewhat funiculose, usually with fairly abrupt, even, circular margin, white at first becoming pale pink; drops sparse, tiny, colourless, or lacking; reverse at first white then gradually turning pale yellow from centre outwards, sometimes shading to pale orange or buff; conidial structures very simple, consisting of single phialides or whorls of phialides occurring irregularly along aerial hyphae, or of short conidiophores, simple or very sparingly branched, bearing terminal whorls of phialides; conidiophores, when present, 7–15 μ long and

1·5–2 μ diam., smooth; phialides in whorls of up to 5, 7–18 μ long by 1–2 μ diam. at base, tapering to a long tube 0·5 μ diam., usually bent fairly sharply; conidia cylindrical with rounded or pointed ends, 3–4 × 1–2 μ, in



Text-fig. 15. *P. fumoso-roseus.* 1, abortive head; 2–6, conidial structures; 7, conidia; 8–10, habit sketches of conidial structures; 11, germinating conidia.

chains which are twisted but seldom tangled one with another, mostly 45–50 μ long but occasionally up to 90 μ.

Colonies on malt agar growing more rapidly than on Czapek, 33–37 mm.

in 7 days and 65–85 mm. in 14 days, otherwise similar except that conidial chains tend to be longer and occasional conidia are larger, $5 \times 2\,\mu$.

Colonies on potato agar spreading slightly more rapidly than on Czapek, 27–39 mm. in 7 days and 55–80 mm. in 14 days, and becoming funiculose more rapidly; conidial chains usually longer than on Czapek and sometimes tending to slime down into irregular masses; occasional conidia up to $5\,\mu$ long.

Conidial production tends to decrease, and the surface colour tends to become paler, on continued cultivation. Slide cultures, incubated at high relative humidity, are abnormal, producing abortive heads with swollen cells in place of phialides, and no conidia.

Conidia tend to elongate before germination, then produce a polar germ-tube. Usually a second tube is put out later and occasionally a third.

Growth is nil at 8° C., very slow and poor at 10–14° C., and nil at 30° C. or over.

Discussion

Found by Wize (1904) on larvae of *Cleonus punctiventris*, in the Ukraine, and named *Isaria fumoso-rosea*. He states that the fungus is characterized by the formation of long, white to yellowish, coremia, and that the spores are lilac pink. His coloured plate shows cultures of a pale pink colour, and his drawings indicate clearly that his fungus was a *Paecilomyces*. His diagnosis has been broadened somewhat to cover other related strains.

Vuillemin (1911) described a new species, *Spicaria aphodii*, which occurred on the bodies of Coleoptera, but grew just as well on vegetable debris, hotbeds, and artificial media. The diagnosis is too brief to be adequate, but, from the figures and the statements regarding colour and size of conidia, there is little doubt that Vuillemin's species is to be regarded as a strain of *P. fumoso-roseus*. A culture received from C.B.S. as *S. aphodii* Vuill. is typical *P. fumoso-roseus*.

Petch (1925) suggested that *S. aphodii* and *S. cossus* Portier et Sartory are synonyms. No culture of the latter species has been available for study but we cannot agree with Petch, since *S. cossus* is described as white to pale cream; also the sporing structures described by Portier & Sartory are more complex than those found in *P. fumoso-roseus*.

Vassiljevski (1929) isolated from pupae of *Hylemyia floralis* and *H. brassicae* two (*sic*) species of *Spicaria*, one non-coremial and identified as *A. aphodii*, the other coremial and identified as *Isaria fumoso-rosea* Wize but transferred to *Spicaria*.

Siemasko (1937) isolated a fungus from *Melolotha melolotha* which he identified as *Spicaria* (*Isaria*) *fumoso-rosea*. He considers that *S. aphodii* and *S. cossus* are synonyms of *S. fumoso-rosea*. His drawings show phialides typical of *Paecilomyces* and he gives the conidia as measuring $2–2{\cdot}5 \times 1{\cdot}5–2\,\mu$.

Kennelly & Grimes (1930) described a *Paecilomyces* from Irish butter. They considered it to be a new species and named it *P. hibernicus*. From their description and figures, and from examination of a culture received from C.B.S. as *P. hibernicus*, obtained by them from the Institute of Dairy Science, Cork, it is concluded that *P. hibernicus* is another synonym of *P. fumoso-roseus*.

From the above it is apparent that *P. fumoso-roseus* is of widespread occurrence, chiefly as a parasite of insects but capable of growing on other substrata.

Material studied

Pa 6. Culture from C.B.S., Nov. 1950, as *Paecilomyces hibernicus* Kenn. et Grimes. Since this isolate came from the Institute of Dairy Science, Cork, it is probably the type strain. We have not seen either coremia or macrospores in our cultures; otherwise there is good agreement with the authors' description.

Pa 38. Culture from C.B.S., Nov. 1951, as *Spicaria aphodii* Vuill., received from Vuillemin. This is quite typical.

Pa 44. Culture from C.B.S., Nov. 1951, as *S. fumoso-rosea* (Wize) Vassilj., obtained from Bondarzew. This strain spores very tardily but eventually produces the typical pink colour. The spore chains show some tendency to slime down into irregular masses. On Czapek agar some enlarged, thick-walled cells are produced, 7–26 × 1·8–2 μ, resembling the tips of the swollen hyphae produced by all strains in slide culture.

Pa 45. Culture from C.B.S., Nov. 1951, as *S. fumoso-rosea* (Wize) Vassilj., C.B.S. isolate. Spores tardily and produces some pink colour only in age.

Pa 51. Culture from H. Stenton of University College, Hull, Jan. 1952, isolated from Wicken Fen soil. Stenton stated that the fungus, when first isolated, produced soft, finger-like coremia. This strain is quite typical and produces the deepest pink colour of all the strains examined. Colonies eventually become very funiculose and, on malt or potato agar, small coremia are sometimes formed.

Herb. Petch, 2 specimens (without numbers) labelled '*Spicaria* (*Isaria*) *fumoso-rosea* (Wize) Vassil., on dead glow-worm'. Both were collected at Wheatfen Broad. The fungus formed long, finger-like coremia, somewhat pinkish. These disintegrated completely on mounting so that no structures could be made out. The size of the spores agreed with our findings.

Section *Compacti*

Paecilomyces carneus (Duché et Heim) comb.nov.

Spicaria carnea Duché et Heim (1931), p. 454.
Paecilomyces austriacus Szilvinyi (1940/41), p. 176, fig. 31.
Spicaria viride Szilvinyi (1940/41), p. 176, fig. 33.
?*Spicaria decumbens* Oudemans (1902), p. 290.

Colonies on Czapek agar at 24° C. growing restrictedly, 12–18 mm. diam. in 7 days and 23–27 mm. in 14 days, consisting of a tough matted basal felt with a thin floccose overgrowth, either remaining floccose or becoming smooth and dusty, sometimes becoming cracked and buckled, at first pure white, eventually developing a pale pink tinge, sometimes with a green tint showing through from the reverse; drops large, sparse, colourless to faint yellow, or lacking; reverse at first dirty white, becoming olive green to dark green, often more or less zoned and shading to white or yellow at the margin, with the colour not diffusing; conidial structures elongated to compact, varying in complexity from single detached phialides to heads with a terminal whorl of phialides and whorls of branches and phialides from lower nodes; conidiophores arising from aerial hyphae, fairly short, or from the basal felt and then up to 150 μ long, 1–2 μ diam., often swollen at the tip to 3–5 μ, septate, smooth; phialides (9) 12–16 (20) μ long, with basal portion cylindrical, 1·5–2·5 μ diam., tapering at just over half the length to a long narrow tube, 0·5–1 μ diam.; conidia broadly

elliptical, finely roughened, 3–4 × 2–2·5 μ, hyaline under the microscope but very pale pink in mass, in chains which are usually less than 100 μ long, divergent, straight or undulate, seldom tangled.

Colonies on malt agar growing at about the same rate as on Czapek, more densely floccose and somewhat funiculose, occasionally producing

Text-fig. 16. *P. carneus*. 1–9, conidial structures; 10–17, habit sketches of conidial structures; 18, conidia.

tiny synnemata; surface colour as on Czapek but reverse white to pale tan; other details as on Czapek.

Colonies on potato agar growing slightly more rapidly, 12–16 mm. in 7 days, and 23–30 mm. in 14 days, more deeply floccose than on Czapek and somewhat funiculose; surface colour as on Czapek; reverse rapidly becoming intense green to almost black in the centre, with the intensity of colour diminishing in zones to a dirty yellow or white margin, the green colour becoming duller with age and eventually fading to a greenish brown; other findings as on Czapek.

The green colour of the reverse of colonies is very distinctive in fresh isolates. It tends to diminish in intensity with continued cultivation.

Spores germinate by one, two, or occasionally three successive germ-tubes.

Growth is exceedingly slow at 8° C., still very slow at 10–14° C., and nil at 30° C. or over.

Discussion

Duché & Heim (1931) describe this species as follows: 'Hyphae cylindric, irregularly septate, 3–5 μ diam. Sporophores erect, bearing verticils of 2–3 branches, each bearing about 3 elongate-fusiform phialides, 11–14 × 3–5 μ. Conidia pink, smooth, suboval, 2·8 × 3·5 μ, separating easily. Odour nil. Habitat: wet sandy soil, hills of Vauville.

On Czapek agar at 22° C.: 7 days 0·5 cm. diam.; somewhat raised, consisting of hyphae which are erect at centre, decumbent at margin; 12 days 1·5 cm. diam.; pale pink, flat in centre, reverse yellow with deep green band and white edge; 21 days pink, with centre raised, reverse centre greenish yellow, then green ring and white edge.'

Duché & Heim's measurements for diam. of phialides are greater than ours, and they describe the conidia as smooth, whereas we find them to be finely roughened. However, their other measurements fall within the range given above, and they describe the typical restricted growth, pink conidia, and green reverse. In order to cover a number of related strains Duché & Heim's diagnosis has been emended and broadened.

Duché & Heim compared their species with other species of *Spicaria*, and pointed out that it is nearest to *S. decumbens* Oud. It is possible that Oudemans had a strain of what we are regarding as *P. carneus*, but his description is very meagre and does not mention any of the highly distinctive cultural characteristics, so that, although his species was undoubtedly a good *Paecilomyces*, it is impossible to place it with any certainty.

Von Szilvinyi (1940/41) described two species from soil which he regarded as new, *Spicaria viride* and *P. austriacus*. From his descriptions there is little doubt that the two, although placed in different genera, do not differ more than would be expected of two isolates of the same species, and that they are both to be regarded as *P. carneus*.

Heim (1940) reported this species as a saprophyte on banana; otherwise it has been found only in soil.

Material studied

Pa 16. (=B.B 132.) Isolated at L.S.H.T.M. from soil by J. H. V. Charles in 1931. This is probably the oldest of the isolates studied and it now spores tardily and produces the green reverse colour only sporadically. When isolated it was quite typical.

Pa 19. Culture received, Nov. 1950, from J. H. Warcup, who isolated it in 1947 from soil, Lakenheath Warren, and stated that it is common in some alkaline soils. Typical.

Pa 27. Isolated from wall of vaults at L.S.H.T.M., May 1950. Colonies are somewhat thin but otherwise typical.

Pa 33. Culture received from H. Stenton, University College, Hull, in June 1951. Isolated from soil, Wicken Fen, Cambridgeshire, and stated to be common in the Fen soil. Somewhat more funiculose than most isolates but otherwise typical and produces good green colour in reverse.

Pa 39. Culture from C.B.S., Nov. 1951, as *S. carnea* Duché et Heim, obtained from Duché and presumably the type strain. Quite typical.

Pa 40. Culture from C.B.S., Nov. 1951, as *S. decumbens* Oud., C.B.S. isolate. Colonies fairly definitely funiculose; otherwise typical.

Pa 56. Isolated at L.S.H.T.M., Sept. 1952, by Mrs S. Marcus, from soil from roadside, Castle Douglas. This is the most recent isolate. It produces abundant conidia and a rich green colour in reverse.

Species of *Paecilomyces* of which cultures have not been available for study. To be accepted provisionally

Paecilomyces burci (Poll.) Thom (1930), p. 548.

Penicillium burci Pollacci (1921), p. 128.

Pollacci's diagnosis is as follows:

Coloniis in agaro cum glucosio cultis, albis, floccosis, dein griseo-avellaneis; hyphis sterilibus ramulosis, hyalinis, septatis, repentibus vel adscendentibus, 6–7 μ diam.; conidiophoris erectis, simplicibus, septatis, hyalinis, 50–110 μ longis, sursum paucos ramulos gerentibus. Ramulis in catenulas conidiorum abeuntibus; conidiis globosis, rariter ellipsoideis, levibus, pallide fuligineis, 4–5 μ diam.

Habit. in parvo tumore mulieris, socia *Acremoniella Berti* n.sp., Florentis. Clarissimo Chirurgo Burci dicatum.

Berti (1922) redescribed this species and discussed its clinical significance. Thom (1930), having examined Pollacci's mould in culture, made the new combination *P. burci*.

Campatelli (1923) inoculated guinea-pigs with the mould but, although there was some growth of hyphae and the production of an abscess-like inflammation, he did not consider it to be a true pathogen.

Negroni (1943) isolated, from a dead butterfly, a fungus which he identified as *P. burci*. He described enigmatic vegetative structures which were swollen, claviform, often bent, with relatively thick membrane, pigmented, and separated from the rest of the hyphae by septa. This description suggests macrospores, but it is impossible to identify Negroni's species with certainty. The dimensions of the conidia and phialides, and the presence of macrospores, would fit *P. varioti*, but colony colour is not stated and the mould is said to produce coremia.

A culture received from C.B.S. as *P. burci* does not fit Pollacci's original

description. It is described above as *P. parvus* Brown et Smith. *P. burci* appears to be a good species, but no authentic material has been available for examination.

Paecilomyces canadensis (Vuill.) comb.nov.

Spicaria canadensis Villemin (1925), p. 97, fig. 1–7.

Vuillemin's diagnosis is as follows:

Mycelio tenuissimo, repente, septato, albo vel luteolo; hyphis fertilibus ramosis; ramis alternis, ultimis brevibus; phialidibus (basidiis auctorum) saepius apice glomeratis, piriformibus, 8–17 × 3 μ; conidiis laxe catenulatis, hyalinis, oblongis, 4–5·4 × 2·8–3 μ. Habitat in larvis et pupis *Stilpnotiae salicis* in Canada occidentale.

Vuillemin states that it is near to *S. aphodii* (= *P. fumoso-roseus*), but the latter forms pink colonies and has smaller conidia. *P. canadensis* is probably related to *P. farinosus*, differing from this in having larger conidia.

Paecilomyces coccosporus (Drechsler) comb.nov.

Spicaria coccospora Drechsler (1941), p. 786.

Drechsler's diagnosis reads:

Mycelium nutritum hyalinum, ramosum, septatum, intra vermiculos nematoideos evolutum, ex hyphis filiformibus 1·5–3·5 μ crassis constans. Hyphae fertiles extra animal emortuum evolutae, ex magna parte erectae vel ascendentes, axe simplices vel parce ramosae, vulgo 25–200 μ longae, 1·5–2·5 μ crassae, septatae, subter septis ramulos conidiferos ferentes; ramulis conidiferis (phialis) saepius 3–5 verticillatis lageniformibus, vulgo 6–12 μ longis, 1·8–2·5 μ crassis, quoque in sterigma circa 0·6 μ crassum abeunte et ex apice sterigmatis 10–20 conidia deinceps gerente; conidiis continuis, hyalinis, globosis, 1·3–1·7 μ diam., in catenulas digestis. *Plectum parvum* necans habitat in humo silvestri prope Butternut, Wisconsin.

The drawings, as well as the description, leave no doubt that this species is a good *Paecilomyces*. No culture has been available for study, but Drechsler's data indicate affinity with *P. farinosus*, from which it differs in having very small globose conidia.

Paecilomyces cossus (Portier et Sartory) comb.nov.

Spicaria cossus Portier et Sartory (1916), p. 700.

This was described from laboratory cultures, obtained from larvae of *Cossus cossus*, as follows (translated):

Hyphae creeping, branched, septate, 3–4 μ diam.; sporophores slightly less in diam. and attenuated upwards, septate, with internodes about 20 μ at base and 6–8 μ at tip, bearing verticils at each node. Branches at upper nodes are phialides; at lower nodes they are rebranched several times before forming phialides. Phialides flask-shaped, with belly 4 × 2·6–3·5 μ, 1 μ diam. at base and 0·2–0·3 μ at tip. Conidia borne in basipetal succession, numerous, ovate, 3·5–4 × 1·5–1·9 μ.

Grows well on all the usual media, including neutral and acid Raulin, but best on carrot or potato. Colonies white, rampant, sometimes forming coremia, becoming chalky or pale cream. Gelatine slowly liquefied. Milk coagulated in 6 days.

Petch (1925) considered this species to be close to, if not identical with, *S. aphodii* Vuill. However, the pink conidial colour of *S. aphodii* (= *P. fumoso-*

roseus) seems to separate the two, although the conidia of both are of approximately equal dimensions. In our opinion *P. cossus* belongs, in all probability, to the *P. farinosus* series. However, until such time as the species can be restudied in culture, the epithet may stand.

Paecilomyces dactylethromorphis Batista et Maia (1955) (in press).

A culture received under this name from Prof. A. Chaves Batista, Pernambuco, arrived too late for adequate study. In appearance colonies strongly resemble those of *P. varioti*, but the sporing structures are more reminiscent of *Penicillium*. On the other hand, it produces abundant macrospores, which are unknown in the typical Penicillia.

Paecilomyces fimetarius (Moesz) comb.nov.

Spicaria fimentaria Moesz (1921), p. 58, fig. 9.

The original diagnosis is:

Effusa, rosea, pulveracea; hyphis sterilibus repentibus, ramosis, septatis, cca. 5 μ cr.; fertilibus suberectis, septatis, irregulariter ramosis; ramis saepe dichotome ramulosis; ramulis ultimis apice acutis; conidiis ellipsoideis, hyalinis, levibus, 6·5–10 × 5–6 μ, in catenulas longas digestis. Hab. in fimo equino, ad pagum Tétény, prope Budapest.

From the description and drawing this would appear to have affinity with *P. varioti*, but the conidia are somewhat large for this species. The pink colour would place it near to *P. fumoso-roseus*, but again the conidia are too large. The species may be accepted *pro tem.*

Paecilomyces heliothis (Charles) comb.nov.

Spicaria heliothis Charles (1938), p. 897.

The original diagnosis is:

Mycelio albo, septato; synnematibus solitariis vel aggregatis, 1–1·5 cm altis; conidiophoris simplicibus vel ramosis, erectis, 3–8 verticilla prophialidium gerentibus; prophialidibus 3–5 verticillatis vel conglomeratis, oblongis 7–8 μ; phialidibus globosis sterigmatibus breviusculis; conidiis variabilibus, ovato-ellipsoideis, in catenulas longas, 3–3·5 × 5–7 μ. In culturis ex *Heliothe obsoleta.*

Charles considered this to be near to *S. farinosa verticilloides* Fron, but sufficiently different to justify the erection of a new species. It is probably one of the *P. farinosus* series, with conidia considerably larger than in the type species. No culture has been seen. Charles recorded the fungus from several states of the U.S.A., but it has not been reported from other sources.

Paecilomyces longipes (Petch) comb.nov.

Spicaria longipes Petch (1937), p. 51.

This species occurred on spiders and, on one occasion, perithecia of a *Torrubiella* were found in association with it. Petch considered it to be the imperfect form of *T. gonylepticida* Möller.

A specimen in Herb. Petch, labelled '*Spicaria longipes* or prox., on spider, Les Mares, Mauritius, 7.5.38. Mamet No. 78', was examined. The insect

bore white coremia terminating in large heads of the *Paecilomyces* type; conidiophores long, with primary and secondary branches; phialides flask-shaped, 6–8 × 1·5 μ with tips about 0·5 μ diam.; conidia cylindrical to fusiform, smooth, 2–2·5 × 1–1·5 μ. These measurements fall within the limits given in Petch's diagnosis. They suggest affinity with *P. farinosus*, but it is impossible to be certain without cultures.

Paecilomyces simplex (Petch) comb.nov.

Spicaria simplex Petch (1936), p. 59.

Petch compared this fungus with *Spicaria penicillata* von Höhnel and *S. perpusilla* Speg., but considered it to differ from both.

A specimen in Herb. Petch, labelled '*Spicaria simplex* Petch, on *Trichia affinis*, Duncombe Park, Helmsley, August 31st, 1935. Type', was examined.

The *Trichia* formed a luxurious, ochraceous to orange-yellow, granular growth on the surface of a piece of bark. This was partially covered by the *Spicaria*, which appeared to be partly funiculose and partly granular. Microscopic examination showed the *Spicaria* to be mixed with a *Cephalosporium*, with characteristic balls of conidia measuring 3 × 1–1·5 μ. The conidiophores of the *Spicaria* terminated in whorls of phialides and bore further whorls of branches and/or phialides from lower nodes; phialides of the *Paecilomyces* type, 8–17 × 2 μ at the broadest part, with long tips about 0·5 μ in diam.; conidia smooth, broad elliptical to subglobose, 2·5–3·2 × 1·8–2·2 μ.

There is no doubt that this is a *Paecilomyces*, but its relationships cannot be determined without cultures.

Paecilomyces smilanensis (Wize) comb.nov.

Isaria smilanensis Wize (1904), p. 722, fig. 8, 9.

The original description is very brief and does not give any details of sporing structures. From the drawings, however, it is clear that Wize had an Isarioid form of a *Paecilomyces*. The conidia, given as 7–8 × 4–5 μ, are much too large for *P. farinosus*, so Wize's name must stand for the time being. It is to be hoped that the fungus will be rediscovered and examined in culture.

Some fungi, mostly described as species of *Spicaria*, but which are probably to be excluded from *Paecilomyces*

P. = *Paecilomyces; Pen.* = *Penicillium; S.* = *Spicaria.*

S. acridiorum (Brongniart et Delacroix) Vuillemin (1911), p. 76. Not a *Paecilomyces* but more probably belongs in *Beauveria*. *Fide* MacLeod (1954) = *B.globulifera* (Speg.) Picard.

Pen. anomalum Corda (1838), p. 18, Tab. XI, fig. 75. Certainly not either *Paecilomyces* or *Penicillium*. Thom (1930) suggests that it may be a *Scopulariopsis* but it is unidentifiable with certainty.

S. arachnoidea Sacc. et Therry apud Saccardo (1886), *Sylloge*, **4**, p. 167. Saccardo cites, as reference, a paper by Therry (*Rev. mycol., Toulouse*, **7**,

p. 245, 1885) but, although the fungus is mentioned and named therein, there is no description. From Saccardo's short description it seems unlikely that this is a *Paecilomyces*, particularly as the spores are described as globose.

S. areneae Sawada (1914), p. 309. The original description is in Japanese, but Prof. S. Shibata, whilst working at L.S.H.T.M., very kindly obtained for us the following diagnosis from the Ministry of Agriculture and Forestry, Tokyo:

The new species is closely related to *S. prasina* (Maubl.) = *Nomuraea prasina* Maublanc, but it is easily distinguished in that the conidiophores of the latter are pale green and narrower (2–3 μ). The oval conidia of the latter species are also different from the new species.

Description: Mycelium develops abundantly on the host, when young white, becoming purplish and brownish grey with age, cottony, septate, 4–5 μ wide. Conidiophores hyalin, slender, not frequently septate, 500 × 3–4 μ, rarely branched. Near the top of the conidiophores there are many short branches. These branches diverge from a main stem 3–5 times. The short branches further diverge several times, alternate or opposite. Polar branch is bottle-shaped, 7–8 × 2–2·5 μ. Conidia are formed in a chain, ellipsoidal or short cylindrical, hyalin, smooth, unicellular, bi-guttulate, 3·5–5·5 × 2–2·5 μ.

There is no mention in the otherwise carefully drawn diagnosis of the beak on the phialides, characteristic of *Paecilomyces*. From its colour it might be close to *Pen. lilacinum*, but this cannot be decided without cultures.

Isaria atypicola Yasuda (1917), p. 208. Details of the coremia are given by Yasuda but he does not describe the sporing structures in detail. He gives the hosts as *Atypus karschii* Doenitz and *Kishinouyeus typicus* Kishida.

American collections, differing from the Japanese in the smaller size of the clava, were examined by Petch (1939). He compares the sporing structures to those of *S. prasina*, but gives the phialides as clavate or cylindrical, obtuse, 4–5 × 2 μ. Petch is of the opinion that the name of the species should be *S.* (*I.*) *atypicola*. He also states that there is little doubt but that it is the conidial state of *Cordyceps cylindrica* Petch.

If the material examined by Petch really represents Yasuda's species it is certainly not a *Paecilomyces*, and, without cultures, its systematic position must remain in doubt.

S. bassiana (Balsamo) Vuillemin (1911), p. 76. Transferred later by Vuillemin (1912) to *Beauveria*, which is undoubtedly the correct genus.

S. clavulifera Petch (1932), p. 238. This is described as purple-grey to ashy, with cylindrico-clavate phialides, narrowing above to a broad, conical, obtuse apex. A drawing bears out the description, and certainly does not suggest *Paecilomyces*.

Herb. Petch R25, labelled '*Spicaria clavulifera* Petch. On spider. Nuwara Eliya, 2–10–26'. This was found to be a very small specimen, on a leaf reverse, covered with a dusty, more or less funiculose growth. Conidia were smooth, rectangular to fusiform, with rounded ends, 6–7 × 1·8–2·5 μ. Phialides were not seen.

The systematic position of this fungus is in doubt, but it is most probably not a *Paecilomyces*.

S. colorans de Jonge (1909), p. 48. Described as the probable cause of

a canker of cocoa. In culture typical *Fusarium* conidia were produced in addition to the *Spicaria* fructifications. Associated with the *Spicaria* were two species of *Nectria*.

Wollenweber & Reinking (1935, p. 37) give *S. colorans* as a synonym of *Fusarium decemcellulare* Brick, the sole representative of the section Spicarioides, and there is little doubt of the correctness of their placing.

Clonostachys compacta Petch (1933), p. 234. Petch considered that this, except for the arrangement of the conidia (obliquely in chains), was a *Spicaria*. His diagnosis gives 'phialidibus ampullaceis vel cymbiformis, rectis vel curvis, supra attenuatis, 9–12 × 2·5–3 μ; conidiis. . .oblongis vel oblongo-ovatis, 5–6 × 2·5–3 μ'.

This is possibly a *Paecilomyces*. It was put in *Clonostachys* solely because of the conidia lying obliquely in the chains, but this partial slipping of the conidia occurs also in *P. elegans*, and occasionally in other species of *Paecilomyces*. Unfortunately the Petch Herbarium contained no specimens for study.

Botrytis delacroixii Saccardo (1892), *Sylloge*, **10**, p. 540. Regarded by Vuillemin (1911) as a *Spicaria* but there is nothing in the original diagnosis to support this view. *Fide* MacLeod (1954), it is a synonym of *Beauveria globulifera* (Speg.) Picard.

S. densa (Link) Vuillemin (1911), p. 76. (=*Isaria densa* Giard.; *Sporotrichum densum* Link). Picard (1914) and Beauverie (1914) consider it to be a *Beauveria*. *Fide* MacLeod (1954), it is synonymous with *B. tenella* (Delacroix) Siem.

Isaria dubia Delacroix (1893), p. 264. Petch transferred this to *Spicaria* as *S.* (*I.*) *dubia*, and stated that it is the conidial state of *Cordyceps gracilis* Mont. et Dur.

Delacroix described and figured spore-bearing structures which were flask-shaped with 1–4 tiny sterigmata, each of the latter bearing one, cylindrical to fusiform, hyaline spore. This suggests a Basidiomycete but, in any case, the fungus is not a *Paecilomyces*, nor a *Spicaria sensu* Petch.

S. elegans (Cda.) Harz var. *muscorum* Grove ex Sacc. (1886), *Sylloge*, **4**, p. 166. (=*S. elegans* Harz *apud* Grove (1885), p. 11). Hughes (1951) discusses the position of this fungus and describes Grove's specimens in Herb. I.M.I. He concludes: 'The systematic position of the fungus would be clearer with fresh specimens at hand. It is, however, reminiscent, generically at least, of the figures and description of *S. fuligonis* F. Moreau (1916)'. If this is so, then it is improbable that the fungus is a *Paecilomyces*.

P. erectus Demelius (1923), p. 78. The description suggests a *Penicillium* rather than a *Paecilomyces*. Colonies are described as blue-green and velvety, and, although the phialides, as figured by the author, are long and slender, they differ in shape very little from other illustrations, in the same paper, of phialides of various species assigned to *Penicillium*.

Thom (1930) suggests that the place of this species is in the Biverticillata–Symmetrica section of *Penicillium*, but we consider that it is more probably to be classified in the Divaricata.

S. (*Isaria*) *erotyli* Petch (1937), p. 41. Petch's diagnosis reads:

Conidiophoris sparsis vel in clavis albis laxis minutis usque 1·5 mm. alt. aggregatis, simplicibus, usque 130 μ alt., 6 μ diam., phialidibus in verticillis duobus vel tribus

capitulum 25–45 μ alt. formantibus; prophialidibus nullis; phialidibus ampullaceis, 6–14 × 2–2·5 μ; conidiis cylindraceis, utrinque rotundatis, 3–5 × 1–1·5 μ. On *Erotylus* sp. (Coleoptera), Trinidad.

It is described as the imperfect stage of *Cordyceps erotyli* Petch.

There is no specimen in Herb. Petch, so, until the fungus is rediscovered, its systematic position must remain in doubt.

Pen. flavum Ém. et Él. Marchal (1921), p. 129. Regarded by Thom (1930) and Raper & Thom (1949) as probably a *Paecilomyces*. However, the phialides are described as scarcely attenuated at the apex; hence it is more probably a *Penicillium*.

S. fuligonis Moreau (1916), p. 36. The growth, on *Fuligo septica*, is stated to be white. The phialides, as figured, are not typical of *Paecilomyces*, but are more suggestive of *Penicillium*.

S. fumosa Ellis et Everhart (1883), p. 97. The original description is as follows:

Hyphae erect, solitary, smoky brown, obscurely septate and mostly swollen at intervals, attached by a small disk-like expansion at base, 70–80 × 3 μ, subverticillately divided above into 2–5, short (7–8 μ) hyaline branches, swollen at base and bearing at their tips a series of oblong, hyaline, continuous, 2·5 × ·75 μ conidia, placed end to end so as to form a continuous chain or necklace, 20–40 μ long and appearing, when examined in the dry state, as a faintly septate continuation of the terminal branches of the hyphae, but quickly separating into its component conidia on the application of water. On the spines of old chestnut-burs.

This is suggestive of *Paecilomyces*, the ultimate branches, swollen at the base, probably being typical phialides. The term 'smoky brown' might indicate what is usually termed dematiaceous, but, on the other hand, it might refer to a shade nearer to that of *P. varioti*. However, the spores are too small for the latter species.

S. griseola Sacc. (1886), *Sylloge*, **4**, p. 167. It is very doubtful whether this species is a *Paecilomyces*, or *Spicaria* in the commonly accepted sense. The phialides are described as 'obclavate', and it largely depends upon the interpretation of this somewhat vague term as to where the fungus must be classified. Bayliss-Elliott (1930) records *S. griseola*, but her description suggests a *Penicillium*.

Isaria harioti Arnaud (1915), p. 20. Not a *Paecilomyces* but possibly a species of *Beauveria*.

S. lateritia Ciferri (1927), p. 91. Following the diagnosis is a suggestion that this species is related to, if not identical with, *S. colorans* de Jonge. However, Prof. Ciferri states in a letter: '*Spicaria lateritia* was only an anomalous, poor strain of *Neurospora sitophila*.... It cannot be taken in consideration in the genus *Spicaria*.'

S. (Isaria) laxa Petch (1937), p. 60. Petch's diagnosis reads:

Clavis fasciculatis, laxis, linearibus, usque 2 mm. alt. 0·1 mm. diam., hyphis 4 μ diam.; conidiophoris brevibus, crassis, 4 μ diam., septatis, prophialides triverticillatos ferentibus; prophialidibus ovalibus, 6 μ alt., 4·5 μ diam.; phialidibus conicis vel ampullaceis, 6–11 × 2–2·5 μ; conidiis fusoideis, leniter curvatis, uno fine acutis, 5–6 × 1 μ. On Coleopterous larvae, North America.

There is no specimen in Herb. Petch, and the species, so far as is known, has not been recorded elsewhere. No change of name is proposed.

S. mori Hara (1954) p. 400. The description is too meagre to decide the status of the species and no culture is available.

S. mucoricola Spegazzini (1899), p. 333. The description is too vague to justify even a guess at the identity of this species. The conidia are said to be occasionally septate. The fungus was found growing on a living *Mucor*, and is stated to be the conidial state of *Melanospora mucoricola* Speg.

S. musticola Naumoff et Kiryalova (1935), p. 362. The name is applied to the conidial state of *Byssochlamys musticola* Naum. et Kiryal. Whether or not the latter is to be regarded as synonymous with *B. fulva* (see p. 39), a distinct name for the conidial state is superfluous.

S. ochracea (Boudier) Vuillemin (1911), p. 76 (= *Isaria ochracea* Boudier). The description suggests that its place is in *Beauveria* rather than in *Paecilomyces*.

S. penicillata von Höhnel (1904), p. 56. This is described as forming verticils of branches and phialides, with the phialides short fusoid, bearing conidia 8–10 × 1·5–2 μ. It is difficult to surmise what the very inadequate description represents, but it is most improbable that the fungus is a *Paecilomyces*.

S. perpusilla Spegazzini (1882), p. 40. Described as having dark coloured conidia, borne in branched chains; hence excluded from *Paecilomyces*.

S. (*Isaria*) *pulchella* Petch nom.nov. (1933), p. 234 (= *Coremium pulcherrimum* Petch (1926)). The new combination was made because Petch, in 1933, considered the fungus to be an isarioid *Spicaria*. The epithet was changed because of its preoccupation by *I. pulcherrima* B. et Br. The description does not suggest *Paecilomyces*, so no change of name is proposed at present.

S. purpurogenes Nadson et Zolkiewicz (1922), p. 1. Described as having tree-like conidiophores, secondary branches like a 'churn staff' in whorls, and conidia elliptical 1·5–2·25 × 2·25–3 μ in chains. It is possible that this is a *Paecilomyces*, but the description is too inadequate to hazard more than a guess.

S. purpuroidea Hara (1954), p. 400. The description is hopelessly inadequate and no culture is available.

S. rectangularis Petch (1933), p. 234. This species was found on lepidopterous larvae, forest north of Anosibe, 1930. The description was drawn up later from a specimen preserved in spirit. It is described as forming yellow synnemata, 1 cm. by 0·4 mm., with spicarioid conidiophores and spores 4–6 × 1–2 μ. Petch comments: 'The description of the conidia may require amendment, as the specimen had been preserved in alcohol, and few conidia were found. In general appearance the fungus resembles *Hymenostilbe sphingum*.'

It seems probable that not only the conidia but the colour of the specimen and dimensions of all parts would be affected by the long immersion in spirit. Identification must await rediscovery of the fungus.

Pen. repandum Sartory et Bainier (1913), p. 367. No culture is available for study. Thom (1930) regards it as probably a *Paecilomyces*, but the drawings do not support this view.

S. rileyi (Farlow) Charles (1936), p. 398 (= *Botrytis rileyi* Farlow (1883),

p. 121; =*Nomuraea prasina* Maublanc (1903), p. 296; =*S. prasina* (Maubl.) Sawada (1919), p. 606). A culture received in November 1951 from the C.B.S. as *Spicaria prasina* (Maubl.) Saw. appears to fit the various descriptions, as does Herb. Petch R.395, labelled '*Spicaria prasina* (Maubl.) Saw. on caterpillar of Vigna, Talpitigalla, Jan. 1928'. Cultures are very slow growing on all media, becoming most typical on corn-meal agar, pale leek green when mature. Sporing structures are irregular, as in most species of *Paecilomyces*, but the shape of the phialides and the green colour suggest affinity with the Divaricata section of *Penicillium* rather than with *Paecilomyces*. No new combination is proposed.

S. rubra (Baquis) Dodge (1935), p. 842. The description is too scanty for recognition.

S. satoi Hara (1954), p. 400. The description is quite inadequate for recognition and no culture or other material is available for study.

S. shirako Hara (1954), p. 400. The same comments apply.

S. silvatica Oudemans (1902), p. 291. The colour, very pale green, resembles that of *P. victoriae* Szil., but the spores are much too large for this species. The dimensions given are unusual for either *Paecilomyces* or *Spicaria*: phialides 20–25 μ long, and conidia 6–12 × 4–6 μ. In addition, Oudemans's illustration does not fit with *Paecilomyces*. Thom (1930) suggests that the fungus might be *Aspergillus terreus* Thom, but this is impossible if the dimensions quoted are correct.

This species is referred to in a number of publications: Saccardo (1906), Rathbun (1918), Chaudhuri & Sachar (1934), Abbott (1926*a*, *b*), Gilman & Abbott (1927), Gilman (1945). In all these the descriptions merely repeat that of Oudemans, or are still more meagre.

S. simplicissimum Oudemans (1903), p. 763. This is regarded by Thom (1930) as a *Penicillium*, and for the present stands as *Pen. simplicissimum* (Oud.) Thom.

S. smithii Oudemans (1903), p. 763. The colony colour is described as cream, the 'ramuli lageniformes (basidiomorphi)' are over 24 μ long, and the conidia subglobose 6 μ in diameter. This is doubtfully a *Paecilomyces* and is impossible to place with the scanty data available.

S. stricta Petch (1944), p. 89. This was recorded as occurring on a spider in England. It is described as having oval phialides, 5–6 × 2–3 μ, and hence is to be excluded from *Paecilomyces*. No specimen was found in Herb. Petch.

Isaria tenuipes Peck (1879), p. 44. As discussed by Petch (1937, p. 58) this has phialides broadly flask-shaped; hence not a *Paecilomyces*.

Isaria unguis Émile-Weil et Gaudin (1918), p. 461. Probably a species of *Candida*; certainly not a *Paecilomyces*.

S. valdiviensis Spegazzini (1910), p. 181. Through the kindness of Prof. Ciferri of Pavia we have received a photo copy of Spegazzini's description. The Latin diagnosis runs: 'Tenuissime effusa candida; hyphae gracillimae simplices v. bifidae; conidia acrogena cylindracea pusilla hyalina.' The rest of the description is in Spanish. It is stated to be common on *Heterosporium tupae* on living *Lobelia bridgesi*. The infected *Heterosporium* colonies show a pale dirty pink colour; the parasite consists of very slender hyphae (25–50 × 1 μ), colourless, flexuous, sometimes without septa, simple

or bifurcate; conidia cylindrical, truncate at the ends ($5–7 \times 1\,\mu$), forming chains at the tips of the branches.

The conidia are of unusual shape and it would be necessary to see the fungus in culture, or at least to examine exsiccata, in order to decide the status of the species.

S. velutiformis Petch (1932), p. 238 (= *S. areneae* Sawada fide Petch (1925), p. 186). Petch isolated a fungus in 1925 which he considered to represent *S. areneae* Sawada. Later, having seen a translation of Sawada's diagnosis, he concluded that his isolate was different from the Japanese one and redescribed it as *S. velutiformis* sp.nov. The diagnosis is as follows:

> Bright rose or purple-rose, becoming rose-purple when dry. Mycelium stout, $3–5\,\mu$ diam., purple-brown. Conidiophores erect, crowded, covering the insect with a dense pile, about $100\,\mu$ high, stout, $3–4\,\mu$ diameter, septate, with several whorls of prophialides and phialides, $16–25\,\mu$ apart; prophialides oblong-oval or clavate, $4–5 \times 2–3\,\mu$; phialides cylindric, narrow-oval or clavate, apex obtuse, $4–4{\cdot}5 \times 2–2{\cdot}5\,\mu$; conidia hyaline, continuous oblong-oval or narrow-oval, ends obtuse, $3–5 \times 1{\cdot}5–2{\cdot}5\,\mu$, or globose, $2–2{\cdot}5\,\mu$. On a spider, Vavuniya, Ceylon, December, 1923; ditto, Hakgala, Ceylon, May 1912; ditto, Nuwara Eliya, Ceylon, January 1st, 1928 and July 15th, 1928.

Petch recorded the species again in 1937 from the Hawaiian Islands and from the Philippines.

Herb. Petch specimen, labelled 'R 378 = R 489. *Spicaria velutiformis*. On spider, Nuwara Elya, 1.1.1928', was examined. It consisted of a leaf, bearing on the under surface a spider, covered with a deep dirty pink to brown, funiculose growth, bearing granular masses of conidia. Conidia were smooth, ovate, $3 \times 1{\cdot}5–2\,\mu$. No details of sporing structures could be made out, indicating that the specimen was too old when dried.

The shape of the phialides, as recorded by Petch, would exclude this species from *Paecilomyces*, but it would be interesting to see a fresh isolate.

S. viridans Sasaki et Nakane (1946), p. 105. A culture received from Japan under this name is *Metarrhizium anisopliae* (Metsch.) Sorokin.

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A major part of the work here described is incorporated in a thesis which

one of us (A.H.S.B) submitted for the degree of Doctor of Philosophy in the University of London, 1953. Copies of the thesis are deposited in the London University Library, Senate House, and the L.S.H.T.M. Library.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. *Spicaria solani*, after Harting (1846).
Fig. 2. Portion of the same, at higher magnification.
Fig. 3. *S. nivea*, after Harz (1871). A highly idealized illustration, showing branched chains of conidia.

PLATE 2

Fig. 1. *Paecilomyces herbarum* Brown et Smith. Sulcate colony in Petri dish. × 0·8.
Fig. 2. *P. herbarum*. Typical conidial structures. × 500.
Fig. 3. *P. flavescens* Brown et Smith. Funicles of hyphae bearing phialides. × 500.
Fig. 4. *P. parvus* Brown et Smith. Conidial structures. × 500.

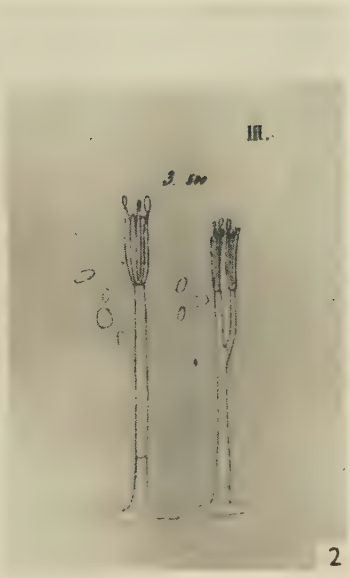
INDEX OF SPECIES

P. = *Paecilomyces*; *Pen.* = *Penicillium*; *S.* = *Spicaria*.

Names accepted are in roman type, rejected names in italics. New names are indicated by an asterisk.

S. acridiorum (Brongniart et Delacroix) Vuillemin (1911), 76
S, aleyrodis Johnston (1917), 50
Pen. anomalum Corda (1838), 76
S. aphodii Vuillemin (1911), 67
S. arachnoidea Sacc. et Therry apud Sacc. (1886) 76
Pen. arenarium Shaposhnikov et Manteifel (1923), 40
S. areneae Petch (1925) [*non* Sawada], 82
S. areneae Sawada (1914), 77
Isaria atypicola Yasuda (1917), 77
P. aureo-cinnamomeus (Biourge) Thom (1930), 40
Pen. aureo-cinnamomeum Biourge (1923), 40
P. austriacus Szilvinyi (1940/41), 70
S. bassiana (Balsamo) Vuillemin (1911), 77
Coremium breve Petch (1926), 50
P. burci (Poll.) Thom (1930), 73
Pen. burci Pollacci (1921), 73
*P. canadensis (Vuill.) Brown et Smith, 74
S. canadensis Vuillemin (1925), 74
S. carnea Duché et Heim (1931), 70
*P. carneus (Duché et Heim) Brown et Smith, 70
Eidamia catenulata Horne et Williamson (1923), 21, 40
S. clavulifera Petch (1932), 77
*P. coccosporus (Drechsler) Brown et Smith, 74
S. coccospora Drechsler (1941), 74
S. colorans de Jonge (1909), 77
Clonstachys compacta Petch (1933), 78
*P. cossus (Port. et Sart.) Brown et Smith, 74
S. cossus Portier et Sartory (1916), 74
P. dactylethromorphis, Batista et Maia (1955), 75
S. decumbens Oudemans (1902), 70
Botrytis delacroixii Saccardo (1892), 78
S. densa (Link) Vuillemin (1911), 78
Corollium dermatophagum Sopp (1912), 18, 21, 40
Pen. divaricatum Thom (1910), 18, 40
S. divaricata (Thom) Gilman et Abbott (1927), 40
S. divaricata (Thom) Ma (1933), 40
Isaria dubia Delacroix (1893), 78
Hormodendron elegans (Corda) Bonorden (1851), 47
Mariannaea elegans Arnaud (1952), 21, 47

1



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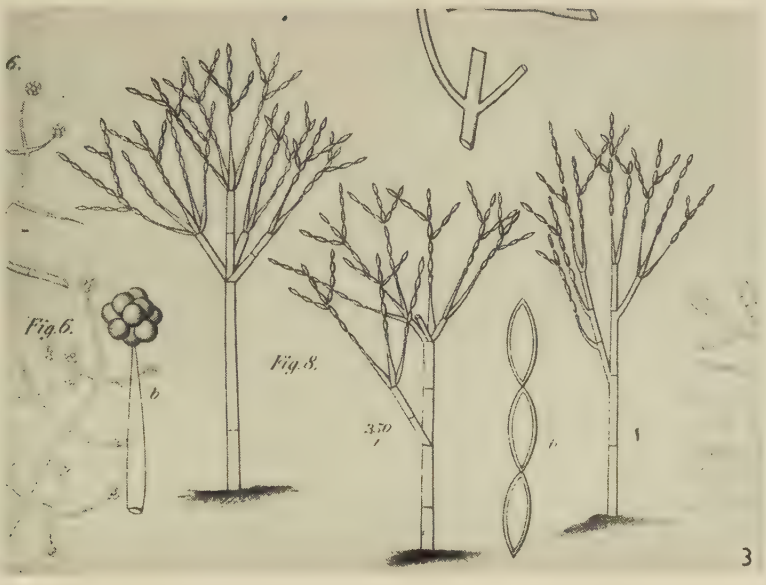

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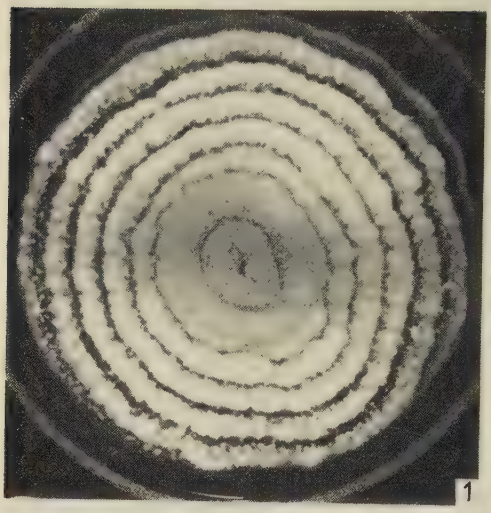
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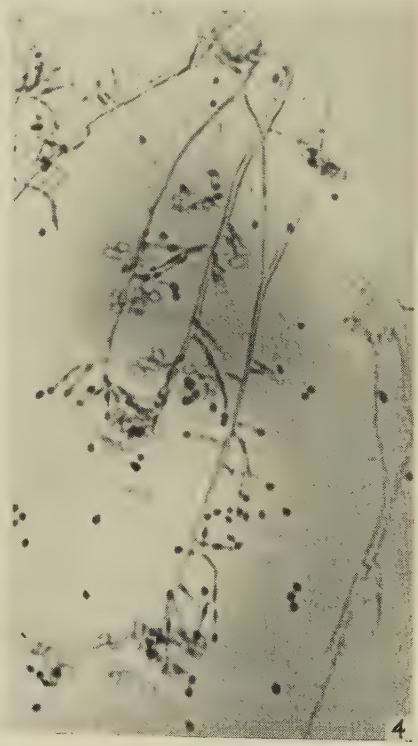
4

P. elegans (Corda) Mason et Hughes (1951), 19, 47
Pen. elegans Corda (1838), 19, 47
S. elegans (Corda) Harz (1871), 47
S. elegans (Corda) Harz var. *flava* Sée (1919), 40
S. elegans (Corda) Harz var. *sorghina* Saccardo (1886), 47
S. elegans (Corda) Harz var. *muscorum* Grove ex Sacc. (1886), 78
P. erectus Demelius (1923), 78
S. (*Isaria*) *erotyli* Petch (1937), 78
Ramaria farinosa Dickson (1790), 50
*P. farinosus (Dicks. ex Fr.) Brown et Smith, 50
S. farinosa (Dicks. ex Fr.) Vuillemin (1911), 50
S. farinosa verticilloides Fron (1911), 50
S. fimetaria Moesz (1921), 75
*P. fimetarius (Moesz) Brown et Smith, 75
*P. flavescens Brown et Smith, 56
Pen. flavum Ém. et Él. Marchal (1921), 79
Monilia formosa Sakaguchi (1939), 40
S. fuligonis Moreau (1916), 79
Byssochlamys fulva Olliver et Smith (1933), 19, 37
S. fumosa Ellis et Everhart (1883), 79
Isaria fumoso-rosea Wize (1904), 67
*P. fumoso-roseus (Wize) Brown et Smith, 67
S. fumoso-rosea (Wize) Vassiljevski (1929), 67
P. fusisporus Saksena (1954), 45
Coremium gracile Petch (1926), 50
S. gracilis (Petch) Petch (1932*a*), 50
S. griseola Saccardo (1886), 79
Isaria harioti Arnaud (1915), 79
*P. heliothis (Charles) Brown et Smith, 75
S. heliothis Charles (1938), 75
*P. herbarum Brown et Smith, 43
P. hibernicus Kennelly et Grimes (1930), 19, 67
*P. javanicus (Fried. et Bally) Brown et Smith, 65
S. javanica Friederichs et Bally (1923), 65
S. javanica Bally *fide* Petch (1925), 67
S. lateritia Ciferri (1927), 79
S. laxa Petch (1937), 79
Pen. lilacinum Thom (1910), 64
*P. longipes (Petch) Brown et Smith, 75
S. longipes Petch (1937), 75
P. mandshuricus (Saito) Thom (1930), 40
P. mandshuricus (Saito) Thom var. *saturatus* Nakazawa, Takeda et Suematsu (1934), 40
Pen. mandshuricum Saito (1921), 40
P. marquandii (Massee) Hughes (1951), 19, 23, 62
Verticillium marquandii Massee (1898), 19, 24, 62
Cordyceps militaris (Fr.) Link *stat. conid.*, 53
S. mori Hara (1954), 80
S. mucoricola Spegazzini (1899), 80
Byssochlamys musticola Naumoff et Kiryalova (1935), 19, 37
S. musticola Naumoff et Kiryalova (1935), 19, 80
Byssochlamys nivea Westling (1909), 19, 35
S. nivea Harz (1871), 22
S. ochracea (Boudier) Vuillemin (1911), 80
*P. parvus Brown et Smith, 58
S. penicillata von Höhnel (1904), 80
S. perpusilla Spegazzini (1882), 80
Nomuraea prasina Maublanc (1903), 81
S. prasina (Maubl.) Sawada (1919), 81
S. pulchella (Petch) Petch (1933), 80
Coremium pulcherrimum Petch (1926), 80
Corethropsis puntonii Vuillemin (1930), 20, 54
P. puntonii (Vuill.) Nannizzi (1934), 20, 54
S. purpurogenes Nadson et Zolkiewicz (1922), 80
S. purpuroidea Hara (1954), 80
S. rectangularis Petch (1933), 80
Pen. repandum Sartory et Bainier (1913), 80
Botrytis rileyi Farlow (1883), 80
S. rileyi (Farlow) Charles (1936), 80
S. rubido-purpurea Aoki (1941), 64
S. rubra (Baquis) Dodge (1935), 81
S. satoi Hara (1954), 81
S. shirako Hara (1954), 81
S. silvatica Oudemans (1902), 81
S. simplicissimum Oudemans (1903), 81
*P. simplex (Petch) Brown et Smith, 76
S. simplex Petch (1936), 76
Isaria smilanensis Wize (1904), 76
*P. smilanensis (Wize) Brown et Smith, 76
S. smithii Oudemans (1902), 81
S. solani Harting (1846), 22
S. stricta Petch (1944), 81
P. subflavus Szilvinyi (1940/41), 50
Coremium swantonii A. L. Smith (1919), 50
S. (*Isaria*) *swantonii* (A. L. Smith) Petch (1931), 50
S. taurica Naumoff et Kiryalova (1935), 40
Isaria tenuipes Peck (1879), 81
S. unguis Émile-Weil et Gaudin (1918), 81
S. valdiviensis Spegazzini (1910), 81
P. varioti Bainier (1907), 17, 40
S. velutiformis Petch (1932), 82
Pen. verticillatum Corda (1837), 21
S. verticilloides Fron (1911), 50
*P. victoriae (Szilvinyi) Brown et Smith, 60
Pen. (*P.*) *victoriae* Szilvinyi (1936), 60
Pen. viniferum Sakaguchi, Inoue et Tada (1939), 40
S. violacea Abbott (1926), 19, 62
S. violacea Petch (1932), 62
S. viridans Sasaki et Nakane (1946), 82
S. viride Szilvinyi (1940/41), 70

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THREE LEAF DISEASES OF YOUNG OIL PALMS ASSOCIATED WITH *HELMINTHOSPORIUM* SPP.

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(With Plate 3 and 3 Text-figures)

Observations on pre-nursery and nursery oil palms in the Belgian Congo have resulted in the identification of three, previously unreported, leaf diseases which have been tentatively named 'Eye Spot', 'Leaf Rot' and 'Leaf Speckle'. Eye Spot and Leaf Rot are allied in that they appear together in the pre-nursery, and double infection of the seedlings is of common occurrence. Eye Spot is caused by *Helminthosporium carbonum* whilst Leaf Rot is associated with the *Helminthosporium* state of *Cochliobolus heterostrophus*. Nurseries and pre-nurseries are commonly established on recently cleared forest and it has been observed that both these fungi are associated with diseases of *Sarcophrynium arnoldianum* (Marantaceae), a plant usually present in the re-growth of cleared forested areas. This host is believed to be a common source of infection for Eye Spot and Leaf Rot of the oil palm. Leaf Speckle has been shown to be caused by a suspected new species of *Helminthosporium*.

Introduction

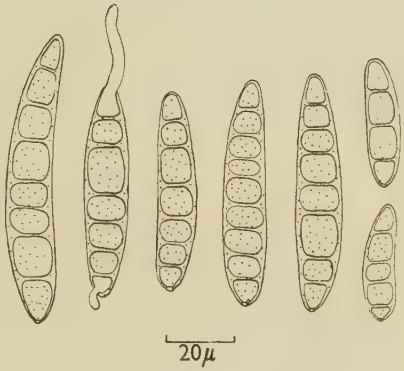
In a previous paper (Kovachich, 1954), a leaf disease of nursery oil palms (*Elaeis guineensis*) caused by *Helminthosporium halodes* was described. Further investigations into the diseases of pre-nursery and nursery oil palms have resulted in the isolation of three more species of *Helminthosporium* which are associated with three, previously unreported, disease conditions. These diseases have, provisionally, been named 'Eye Spot', 'Leaf Rot' and 'Leaf Speckle'. These diseases and the associated fungi are described in this paper.

Eye Spot

This disease was first observed in 1954 at Yaligimba and has since been observed at Leverville and Yangambi. Both pre-nursery and nursery palms are susceptible but the disease ceases to be of economic importance six months after the palms are transplanted to the nursery. The disease is not fatal but it may be responsible for a marked reduction in the growth of the young palms.

Infection may occur on all leaves of young palms but the 'spear' leaf and the youngest open leaf appear to be most susceptible. The first sign of infection is the presence of pin-point yellow spots on the laminae. A narrow band of the leaf tissue around these spots then becomes chlorotic. This is followed by the necrosis of the central spot and the enlargement of the chlorotic zone which forms a well-defined 'halo' around the infection point. The disease spot finally consists of a brown, sunken point which

seldom exceeds 0·5 mm. in diameter surrounded by a round to oval-shaped 'halo' which measures 5–7 mm. in diameter. The 'halo' is a pale green colour on the young leaves but on older leaves it may be a marked yellow or orange colour. In cases of heavy infection, adjacent disease spots may coalesce and this results in infected leaves having a chlorotic appearance. Occasionally the whole of the disease spot becomes necrotic. No conidia have been observed in association with the disease spots. Pl. 3, fig. 1, shows a heavily infected leaf of a nursery palm.



Text-fig. 1. Conidia of *Helminthosporium carbonum* from infected leaves of *Sarcophrynium arnoldianum*.

Cultures of recently diseased tissue resulted in the isolation of *H. carbonum*. When a spore suspension of this fungus was sprayed over young oil palms the disease was reproduced and the fungus was re-isolated from the infected seedlings. As no conidia were associated with the disease spots the possibility of an alternative host was considered. A disease with similar symptoms was found on a plant known locally as Ngungu (*Sarcophrynium arnoldianum* (Marantaceae)). It was found that conidia of *Helminthosporium carbonum* were associated with this disease and when a spore suspension of conidia from this host was sprayed on young oil palms, typical disease symptoms of Eye Spot Disease were reproduced. As *Sarcophrynium arnoldianum* is a common weed in oil palm nurseries and around pre-nursery sites, it is considered that this plant is a common source of infection for the disease of oil palms.

Helminthosporium carbonum Ulstrup (Text-fig. 1)

On *Sarcophrynium* leaves, conidiophores occurred singly or in pairs, they were a pale brown colour with the distal ends almost hyaline and, occasionally, forked. They were 78–185 μ long and 5–6 μ wide with an enlarged basal cell. The conidia were cylindrical, slightly curved, hyaline to pale olivaceous-green with darker coloured basal scars. They were 3–8 septate and measured 36–86 μ long and 11–14 μ wide. Germination tubes were hyaline and developed from the terminal cells. In culture the conidia were a dark, olivaceous brown colour.

Leaf Rot

Serious outbreaks of this disease have been observed at Yaligimba and Mombesa in the Belgian Congo. In both localities the disease was associated with the Eye Spot condition and many of the young palms were infected by both diseases. Palms may become infected in the pre-nursery or shortly after transplanting to the nursery. The disease is rarely fatal, but it frequently destroys a considerable part of the leaves so that pre-nursery seedlings become unfit for transplanting and nursery palms suffer a set-back from which they rarely recover.

Early symptoms of infection are similar to those of Eye Spot except that the pin-point spots are much more numerous. These spots become brown and necrosed with a very small, chlorotic halo around their periphery.

Text-fig. 2. Conidia of *Cochliobolus heterostrophus* from diseased leaves of young oil palms.

Unlike Eye Spot, the necrosed spots commonly enlarge and coalesce with neighbouring spots giving rise to a general rotting of the leaf. The distal ends of the leaves are generally most heavily infected and are the first parts to become rotted. The rot spreads downwards towards the base of the leaf as more infection spots appear on the leaf. A characteristic symptom of the disease is a general chlorosis of parts of the leaf which are heavily infected but not rotted. The rotted parts of the leaves are a dark brown colour and frequently shred. Pl. 3, fig. 2, illustrates an infected nursery seedling.

Conidia associated with the rotted leaves of pre-nursery palms were identified as the *Helminthosporium* state of *Cochliobolus heterostrophus* (Drechsl.) Drechsl. The same fungus was also found associated with a similar type of rotting of *Sarcophrynium* leaves. No pathogenicity tests have been carried out as it has not been possible to obtain the fungus in pure culture.

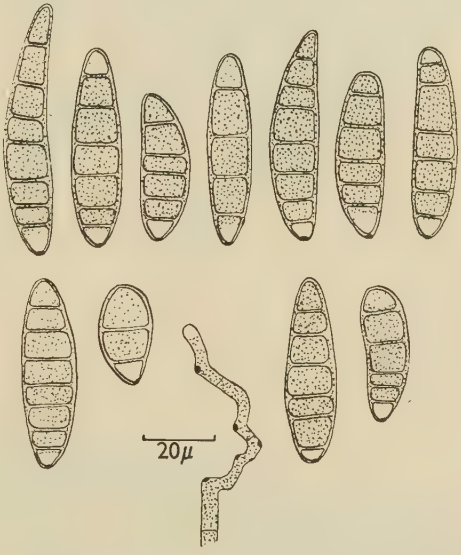
Cochliobolus heterostrophus (Drechsl.) Drechsl. (Text-fig. 2)

Conidiophores were scattered and appeared singly. They were a pale brown colour with the distal end almost hyaline, and the basal cell was enlarged. They measured 120–170 μ long and 5–6 μ wide. The conidia

associated with the rotting of young oil palm leaves were cylindrical to obclavate, a pale olivaceous-green colour and possessed a slight basal scar. They were 6–12 septate and measured 60–120 μ long and 11–14 μ wide. Conidia from *Sarcophrynium* leaves were 3–9 septate and 40–120 $\mu \times$ 11–14 μ.

Leaf Speckle

This is an unimportant disease of pre-nursery seedlings which has been observed at Yaligimba. The symptoms consist of scattered, brown, pin-point spots similar to the early stages of the two previously mentioned diseases, but there is no chlorosis of the adjacent tissue and the necrosed spots do not enlarge. Occasionally the infection spots are numerous in localized areas of the leaves, usually at the distal end or the centre of the



Text-fig. 3. Conidia and a conidiophore of the *Helminthosporium* sp. causing Leaf Speckle of young oil palms.

leaf, and in such cases the necrosed spots may coalesce giving rise to a localized rotting of the leaf. No conidia have been observed in association with this disease but a species of *Helminthosporium* has been commonly isolated from the diseased tissue. When a spore suspension of this fungus was painted on the leaves of young palms the disease spots were reproduced but the rotting of the leaves has not been reproduced by inoculation. A culture of this fungus was forwarded to the Commonwealth Mycological Institute. Dr M. B. Ellis reported that it did not exactly match up with any species of *Helminthosporium* in the herbarium of that Institute, as although many of the conidia have a thickened sometimes dark-coloured septum at one or both ends and paler end cells characteristic of the *halodes* group, there is no projecting basal hilum (Text-fig. 3).

In culture, the mycelium is largely superficial on the substratum with hyaline to pale brown mycelium 2–6 μ wide. Conidiophores appear singly,

are pale brown, often geniculate with several well-defined scars and are 55–160 μ long. Conidia are pale brown to dark brown with the basal cell frequently almost hyaline and the distal cell also a paler colour. They are cylindrical to obclavate with a basal scar, 2–8 septate and measure 25–75 $\mu \times$ 13–16 μ. A culture has been disposed at the Commonwealth Mycological Institute as IMI 61030.

I am indebted to the Plantations Executive of Unilever Limited for permission to publish this report and to Dr M. B. Ellis for the identification of *Helminthosporium carbonum* and *Cochliobolus heterostrophus*.

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EXPLANATION OF PLATE 3

Fig. 1. A leaf of a nursery oil palm infected with Eye Spot disease.
Fig. 2. A young nursery palm infected with Leaf Rot.

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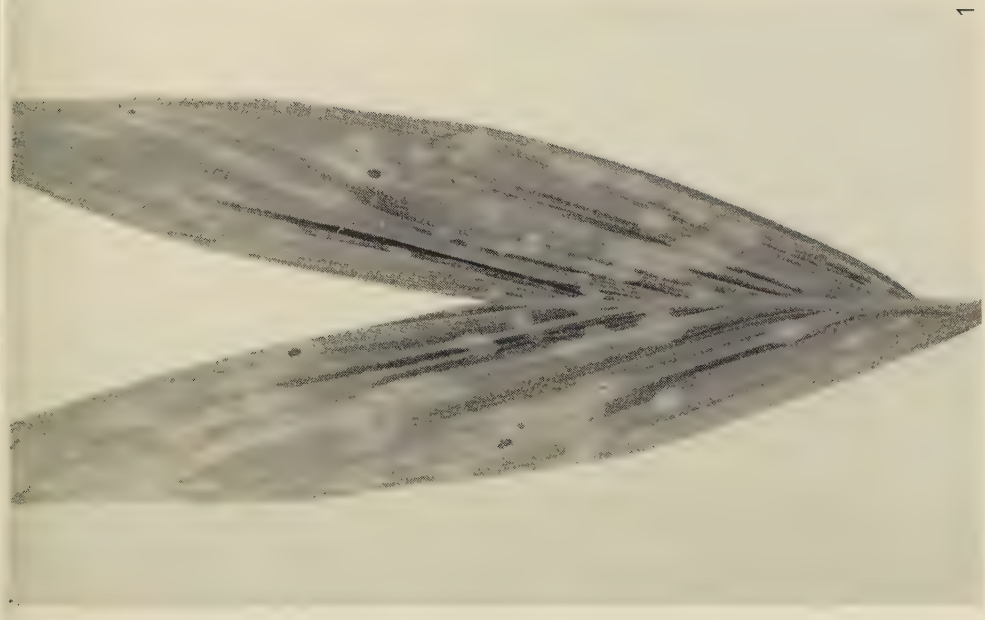

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(*Facing p.* 94)

Trans. Brit. mycol. Soc. **40** (1), 95–108 (1957).

STUDIES ON *PELLICULARIA FILAMENTOSA* (PAT.) ROGERS

II. OCCURRENCE AND DISTRIBUTION OF PATHOGENIC STRAINS

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(With Plate 4)

The pathogenicity to five host families of sixty-eight isolates of *Pellicularia filamentosa* and twelve isolates of *P. praticola* obtained from England and South Australia was examined. Fifty-four isolates of *P. filamentosa* attacked stem structures and, of these, forty-nine were specialized in their attack to one or, in a few cases, two host families. Four attacked more than two host families, and one was non-pathogenic. Thirteen isolates attacked only roots with no evidence of host specialization.

At temperatures above 18–20° C., *P. praticola* isolates attacked the stems of all hosts, but below this temperature only beet was attacked.

Strains specialized to particular hosts frequently occurred when the host was grown as a regular crop; a strain specialized to Cruciferae was present in each of five soils although cruciferous crops were grown only in two of them.

In general there was no correlation between cultural characters and pathogenicity, but in any one soil isolates of the same strain, with few exceptions, were identical in cultural appearance and easily distinguished from other strains.

Introduction

During the last fifty years a wide variety of isolates of *Rhizoctonia solani* Kühn has been obtained. These isolates, although possessing the general vegetative characters ascribed to *R. solani*, have differed markedly from each other in cultural appearance and pathogenicity to different hosts. In the absence of the perfect stage it has been suggested that these isolates may include several species, but the more general view is that they are different strains of the species attacking potato, namely *Pellicularia filamentosa* (Pat.) Rogers.

Flentje (1956) recorded the development of the perfect stage of twenty-eight different isolates of *Rhizoctonia solani* selected from a large number of isolates obtained from England and Australia which, in previous pathogenicity and cultural studies, had been subdivided into seven pathogenic strains. The basis of selection was to obtain a representative of each pathogenic strain, but where a strain included isolates from separate localities in England and Australia or isolates showing markedly different cultural characters, representatives covering these differences were included. Of the twenty-eight isolates, twenty-four were identified as *Pellicularia filamentosa* and the remaining four as *P. praticola* (Pat.) Flentje.

As these twenty-eight selected isolates appeared to cover the variation expressed by the whole range of isolates, these latter were then separated

on the basis of cultural characters into the two species *P. filamentosa* and *P. praticola*. This paper records the study of the pathogenic and cultural characters of the wide range of isolates, the separation of pathogenic strains within *P. filamentosa* and the occurrence of the two species in five different soils.

Literature

The wide host range of *Rhizoctonia solani*, together with the infrequent occurrence of the perfect stage, has led to many studies on cultural and physiological variation. These were comprehensively reviewed by Kernkamp, de Zeeuw, Chen, Ortega, Tsiang & Khan (1952), who concluded that there is an indefinite number of cultural or physiological races, differing in such cultural characters as colour, type of aerial mycelium, zonation, abundance and type of sclerotia and hyphal diameter, or physiological characters such as enzyme production, growth rate and response to temperature, nutrient supply and hydrogen-ion concentration. Richter & Schneider (1953) observed a correlation between the temperature relations of different strains and the conditions in their native habitats.

Fewer studies have been carried out on pathogenic variation, especially the aspects of specialization to different hosts as distinct from varying degrees of attack on the one host. From the review of Kernkamp *et al.* (1952), there appears to be an indefinite number of pathogenic strains, varying from unspecialized strains to strains showing specialization to different varieties of potato.

Attempts have been made to correlate cultural characters with pathogenicity, but with varying success. Houston (1945) indicated some correlation but it appears likely that his type A isolates were *Pellicularia praticola* rather than *P. filamentosa*. Failure to distinguish between these two species has probably complicated the problem of relationships between strains, as suggested by Vanterpool (1953). Exner (1953) suggested that there was sufficient correlation to establish *formae speciales* for four pathogenic strains but her single basidiospore cultures yielded many exceptions, as did her original tissue isolates. Richter & Schneider (1953) separated isolates on their ability to anastomose with each other and indicated a correlation between anastomosing, cultural and pathogenic groups. However, recent genetical studies by Holloway (1955) on *Neurospora* showing that ability to anastomose depends on a small number of genes suggests that this ability may not give a real indication as to how closely isolates are related. Chen's finding, reported by Kernkamp *et al.* (1952), that a variant of *Rhizoctonia solani* failed to anastomose with other variants from the same parent detracts somewhat from the importance of Richter & Schneider's work.

Previous work on variation of *R. solani* has been carried out on isolates obtained from a wide variety of unrelated sources. As far as we are aware, no attempt has been made to study this problem from the ecological point of view, by investigating the occurrence of different strains in one soil and comparing their pathogenic and cultural characters.

Source and identity of the isolates

Isolates of *R. solani* were collected:

(*a*) To investigate the range of isolates occurring generally in England and South Australia; for this purpose, infected plants, or cultures isolated from infected plants, were obtained from other workers.

(*b*) To investigate the range in localized areas; five soils, in which the crops were being attacked by *R. solani*, were chosen. The crops were: lettuce at Slough, England; wheat at Norfolk, England, and Cungena, South Australia; cabbage at Bristol, England, and Adelaide, South Australia. Isolations were made from diseased plants grown in the field. In addition, soil samples were taken. The moisture percentage of each sample was raised to approximately 75 % of the field capacity, and seeds of bean, cabbage, lettuce, pea, spinach, sugar beet, tomato, wheat and zinnia, previously surface sterilized with mercuric chloride, were sown in each soil. The pots were covered with metal lids after planting, partly to maintain a constant moisture level and partly because previous work had shown that seedlings grown like this in the dark became infected with a wider range of strains than would infect them when grown under normal light intensities. Seedlings showing lesions were plated on soil-extract agar and a number of isolates was obtained from each soil. As previous examination had revealed no trace of seed-borne *Rhizoctonia*, it was assumed that the isolates had come from the soils.

It was impracticable to study all the isolates obtained from each soil; a selection was made by growing the isolates in culture, and where more than five from one soil appeared identical, only five of these were retained for further study (Table 1).

Soils

The five selected soils from which isolates of *R. solani* were obtained are described in Table 2.

Comparison of pathogenicity

Pathogenicity to widely different hosts was used as the basis for separation of isolates into pathogenic strains, rather than variations in severity of attack on any single host plant. For practical reasons the number of hosts which could be used was restricted and five (each from a different family), wheat, lettuce, tomato, sugar beet and cabbage, were selected as the standard differential hosts.

According to previous workers *Pellicularia filamentosa* attacks the stems or hypocotyls of most plants, but Samuel & Garrett (1932), Hynes (1937) and Blair (1942) had shown that the attack on cereals by some isolates is confined to the roots. For this reason two methods of pathogenicity testing were employed:

(i) Isolates were grown for 10 days at 25° C. on potato-dextrose agar, by which time they had covered a 9 cm. Petri dish, from which disks 2·2 cm. in diameter were cut out for inoculum. Seedlings were grown

Table 1. *Designation of source and isolates*

(*a*) Isolates from seedlings in five selected soils

Isolation no.	Isolated from seedlings with	Area of origin
1–10	Damping off	Bristol, England
11–20	Damping-off and foot rot	Cungena, South Australia
21–30	Damping off and foot rot	Norfolk, England
31–47	Damping off	Slough, England
48–52	Damping off	Adelaide, South Australia

(*b*) Isolates from scattered sources

Isolation no.	Source	Isolation no.	Reference to Paper I
53	Potato stem lesion, London, England	16–18	RT 2–RT 4
54	Potato stem lesion, Cambridge, England	31, 42	Co, ST 1
55	Potato stem lesion, Bristol, England	—	—
56	Potato stem lesion, Woodside, South Australia	56	So 4
57	Potato stem hymenium, Woodside, South Australia	57	So 5
58	Tomato stem lesion, Cheshire, England	58	So 1
59	Tomato stem lesion, Cheshire, England	59	So 3
60	Tomato stem lesion, Brough, England	—	—
61	Tomato stem lesion, Leeds, England	61	So 2
62	Tomato stem lesion, High Wycombe, England	—	—
63	Tomato stem lesion, Bristol, England	—	—
64	Tomato stem lesion, Adelaide, South Australia	—	—
65	Tomato stem lesion, Adelaide, South Australia	—	—
66	Cauliflower stem lesion, Lancashire, England	—	—
67	Cabbage stem lesion, Bristol, England	—	—
68	Cabbage stem lesion, Hitchin, England	68	CR 1
69	Cabbage stem lesion, Clare, South Australia	69	CR 2
70	Cauliflower stem lesion, Adelaide, South Australia	—	—
71	Wheat root lesion, Hitchin, England	—	—
72	Barley root lesion, King's Lynn, England	72	RT 1
73	Oat root lesion, Keith, South Australia	73	RT 5
74	Clover root lesion, Keith, South Australia	74	RT 6
75	Wheat stem lesion, Ceduna, South Australia	—	—
76	Clover stem lesion, Keith, South Australia	76	ST 2
77	Dahlia stem lesion, Leeds, England	—	—
78	Petunia stem lesion, Adelaide, South Australia	—	—
79	Celery stem lesion, Leeds, England	—	—
80	Pea stem lesion, Murray Bridge, South Australia	80	NP 1

Table 2. *Five soils used for detailed isolations*

Locality	General character	pH	Water-holding capacity, % of oven-dry soil	Field capacity, % of oven-dry soil	Cropped to
Slough, England	Red brown medium loam	5·3	42·5	23·2	Lettuce
Norfolk, England	Grey sandy loam	6·4	28·1	17·1	Wheat
Bristol, England	Red brown sandy loam	6·6	26·3	15·4	Lettuce and cabbage
Cungena, South Australia	Dark brown calcareous sandy loam	8·9	38·4	20·9	Wheat and oats
Waite Institute, South Australia	Heavy red-brown silt loam	6·5	41·8	22·5	Wheat

in cylindrical glass jars, approximately 9 cm. in diameter and 9 cm. high, half filled (350 g.) with soil; ten seedlings were established per jar in a circle 5 cm. in diameter. The inoculum disks were placed in the centre of each circle, approximately 0·5 cm. below the soil level, and covered with soil. Four replicates were used and the jars were covered with moisture-proof cellophane throughout the work to maintain the soil moisture level constant at approximately 75 % field capacity. Pathogenicity was measured by recording the number of seedlings which 'damped off' or showed necrotic lesions.

(ii) Isolates were grown in 500 ml. Erlenmeyer flasks on a sterilized mixture of sand and maize-meal (95 % sand, 5 % maize meal, with distilled water to 15 % moisture). After 15 days' incubation at 25° C., this inoculum was mixed into soil at the rate of 5 % and the soil moisture was adjusted to approximately 75 % field capacity. After placing this inoculated soil in the glass jars described above, enough seeds to give ten seedlings of the various hosts were planted 1 cm. deep in the soil and the jars were covered with moisture-proof cellophane. Four replicates were used and pathogenicity was measured by removing all seedlings after 3 weeks, recording damage to the roots and measuring the height of seedlings.

Samples of all seeds were examined prior to sowing to make certain they carried no infection of *P. filamentosa* or *P. praticola* in the seed itself. Natural soil known to be free from *P. filamentosa* and *P. praticola* was used. By means of a series of pilot experiments using a range of soil moisture levels it was shown that at 75 % field capacity *P. filamentosa* and *P. praticola* grew through the soil satisfactorily, but that there was no significant damage from other damping-off fungi such as *Pythium* which might be in the soil.

Simultaneous testing of all isolates was not possible and preliminary tests were carried out to scan the variation in pathogenicity and to obtain a range of pathogenic strains which could be used as a common reference for all later pathogenicity tests. Four isolates of *Pellicularia filamentosa*, 31, 61, 56 and 72, and one of *P. praticola*, 42, which showed marked differences in pathogenicity, appeared to cover the main range of pathogenicity and these were selected as reference strains.

Isolate 31

Lettuce. Severe rotting of hypocotyl and root near soil level, rapidly extending through entire plant. 100 % plants affected. *Cabbage.* As for lettuce above but much slower extension through entire plant. 20–30 % plants affected. *Tomato, sugar beet, wheat,* No effect.

Isolate 66

Lettuce. Occasional yellow-brown lesions on hypocotyl, usually superficial but occasionally deep; where such lesions coalesce, seedlings are killed. No extension beyond lesions. 1–10 % plants seriously affected. *Cabbage.* Severe rotting of hypocotyl and root near soil level, rapidly extending through entire plant. 100 % plants affected. *Tomato, sugar beet, wheat.* No effect.

Isolate 61

Lettuce, cabbage. No effect. *Tomato.* Severe rotting of hypocotyl and root near soil level, slowly extending through entire plant. 90–100 % plants affected. *Sugar beet, wheat.* No effect.

Isolate 72

All five hosts. Roots severely rotted, but no extension into stem. Stunted plants remain alive. 100 % plants affected.

Isolate 42 (*P. praticola*)

Lettuce, cabbage, tomato, sugar beet. Above 18–20° C. Severe rotting of hypocotyl and roots near soil level, rapidly extending through entire plant. 100 % plants affected. *Below* 18–20° C. Superficial yellow-brown lesions on lettuce hypocotyl. No extension in the plant. 10–50 % plants affected. No effect on cabbage and tomato. Rotting of hypocotyl of sugar beet and slow extension through the plant. 20–50 % plants affected. *Wheat. Above* 18–20° C. Red-brown eyespot lesions on the coleoptile. 50–100 % plants affected. *Below* 18–20° C. No effect.

The effect of isolate 72 on roots compared with the lack of effect by the other isolates is illustrated in Pl. 4, fig. 1; the lesions produced by *P. praticola* (isolate 42) on wheat above 20° C., are illustrated in Pl. 4, fig. 2.

These reference isolates were tested over a range of soil temperature and moisture conditions, and in soils varying in texture from light sands to heavy clay loams. Temperature was the only factor which influenced pathogenicity, and then only in the case of *P. praticola*, as described above.

Reference isolate 31, although pathogenic to cabbage, was far more severe on lettuce, while isolates 66 and 61 were specific to cabbage and tomato, respectively. To determine whether this specificity was to host families rather than to individual species, the pathogenicity of these isolates was tested on other members of the three host families—Compositae, Cruciferae and Solanaceae. As the first supposition proved to be correct, isolate 31 was thereafter regarded as a composite strain, isolate 66 as a crucifer strain, and isolate 61 as a solanaceous strain.

The remaining reference isolate of *P. filamentosa*, 72, was regarded as a root strain, because of its specialization on roots and failure to attack stems.

Following this preliminary work the pathogenicity of all isolates was tested in a series of experiments in which the temperature was maintained at or above 20° C., and other factors kept as nearly constant as possible. In each experiment the four reference isolates of *P. filamentosa* and *P. praticola* were included, together with appropriate controls. All the isolates listed in Table 1, with the exception of six which are discussed later, agreed closely in pathogenicity with one or other of the five reference strains.

The six isolates which were not identical in pathogenicity with any of the five reference isolates were isolates 47, 62, 75, 78, 79 and 80; the details of their pathogenicity to the differential hosts are set out below:

Isolate 47

Lettuce, cabbage, tomato, sugar beet. Severe rotting of stem and root near soil level, gradually extending throughout the plant. 50–80 % plants affected. Not influenced by temperature above or below 20° C. *Wheat.* No effect.

Isolate 62

Lettuce, cabbage, tomato. Severe rotting of stem and root near soil level, gradually extending throughout the plant. 50–80 % of plants affected. Not influenced by temperature above or below 20° C. *Sugar beet, wheat.* No effect.

Isolate 75

Lettuce. Yellow-brown lesions on stem around soil level causing collapse of seedling, but very slow spread up and down seedling axis. 100 % plants affected. *Cabbage.* No effect. *Tomato, sugar beet.* As on lettuce, but rapid spread in seedlings. *Wheat.* Yellowing and distortion of young leaves, which emerge from the soil curled in spiral, or at varying angles between horizontal and vertical. Secondary roots severely rotted. 30–60 % plants killed.

Isolate 78

Lettuce. Yellow-brown lesions on stems near soil level, causing collapse of seedlings. No spread up and down the seedling axis. *Cabbage.* No effect. *Tomato.* Severe rotting of stem cortex near soil level, and no (or very slow) spread up and down seedling axis. 50–80 % seedlings affected. *Sugar beet, wheat.* No effect.

Isolate 79

Lettuce. Yellow-brown lesions on stems near soil level, causing collapse of seedlings. Little or no spread up and down seedling axis. *Cabbage.* No effect. *Tomato, sugar beet.* Severe rotting of stem near soil level, and spread up and down seedling axis. 80–100 % seedling affected. *Wheat.* No effect.

Isolate 80

No effect on any of the five hosts.

These results show that of the fifty-four isolates of *P. filamentosa* which attack stem structures, forty-nine were specialized in their host range and could be separated into three pathogenic strains. Six of them attacked hosts in the Compositae severely and cruciferous hosts mildly, thirty attacked cruciferous hosts only, and twelve attacked only hosts in the Solanaceae. The remaining five stem-attacking isolates, 47, 62, 75, 78 and 79, were much less specialized, each severely attacking hosts from two, three or four different host families. Amongst these five, isolates 47, 62, 78 and 79 were individual isolates which the authors only obtained once during this

work, and nothing is known of their distribution and importance; isolate 75 has since been obtained from wheat crops in several areas of South Australia, where it has caused local but severe losses.

The thirteen isolates of *P. filamentosa* which attacked root structures only showed no specialization in regard to different hosts, although they were less severe on lettuce than on other hosts. Unlike the stem-attacking strains which subsequently grew down into the roots, killing the seedlings, the root strain remained localized in the roots, and top growth of the plants continued, though stunted.

Only one isolate (80) of *P. filamentosa* proved non-pathogenic to any of the host crops tested. The pathogenicity of this isolate was tested to the range of plants, cultivated or otherwise, growing in the area whence it was isolated; as it proved non-pathogenic to these plants also, it is tentatively regarded as a purely saprophytic strain.

The twelve isolates of *P. praticola* were all identical in pathogenicity, and were readily distinguished from isolates 47, 62, 75, 78 and 79 of *P. filamentosa*, which were somewhat similar in pathogenicity, by differences in pathogenicity to cabbage, sugar beet and wheat, and by the absence of any effect of temperature on pathogenicity.

Pathogenic strains in different soils

From Table 3 it appears that the isolates obtained from scattered sources were, with few exceptions, restricted in pathogenicity more or less to the host family from which they were originally isolated, suggesting that where a particular crop is frequently grown a strain specialized to that crop in its parasitism may develop. This method of collecting isolates gives little or no indication as to what other strains exist in the particular soil.

The technique of making extensive isolates from one soil by growing a variety of seedlings in that soil, and isolating from any which develop lesions, gives some idea of the range of strains occurring but it may have limitations imposed by the number of hosts used. These limitations were partially removed by growing the seedlings in the dark, as under these conditions specificity of strains is at least partially broken down and a wide range of isolates will attack any one host. A second limitation is that non-pathogenic strains such as isolate 80 described earlier may be missed. Despite these limitations the isolations showed that the cruciferous strain which damped-off cabbage seedlings occurred in all five soils, irrespective of whether a cruciferous crop was grown there frequently or not. The strain which damped-off lettuce occurred only in the soil at Slough, and not at Bristol where lettuces were also grown regularly. The root-attacking strain, although not restricted to cereal roots, occurred only in the soils at Norfolk and Cungena, where cereals are a frequent crop. *P. praticola* occurred only in the Slough and Bristol soils. These results are set out in Table 3 below.

The technique for isolating the various strains was not designed to yield information on the populations in the different soils, but in all cases twenty to thirty isolates of each strain were obtained from a 5 kg. sample of the soil, indicating that they were relatively abundant.

Table 3. *Grouping of isolates apparently identical in pathogenicity*

	Other isolates agreeing with reference isolate					
	From five selected soils					
Reference isolate	Bristol	Cungena	Norfolk	Slough	Adelaide	From scattered sources
Isolate 31, composite strain	—	—	—	31–36	—	—
Isolate 66, crucifer strain	1–5	11–15, 20	21–25	37–41	48–52	All isolates from cabbage and cauliflower stems, 66–70
Isolate 61, solanaceous strain	—	—	—	—	—	All isolates from tomato or potato stems except 62. 53–61, 63–65
Isolate 72, root strain	—	16–19	26–30	—	—	All isolates from cereal and clover roots. 71–74
Isolate 42, *P. praticola*	6–10	—	—	42–46	—	76, 77

Comparison of cultural characters

Isolates were grown on four different media to determine which of them were closely similar in cultural and morphological characters. No attempt was made to study their nutrient requirements, or to investigate fully the influence of such factors as temperature on growth, although isolates were grown at several temperatures to obtain an indication of whether optimum temperature for growth did vary. The four following media, three of them 'synthetic' media varying in type of nitrogen and in concentration of nitrogen and carbohydrate, and the fourth a 'natural' medium containing potato extract, were used throughout. The composition of the media is set out in Table 4. All cultures were grown at 25° C.

Table 4. *Composition of media for comparison of cultural characters in isolates of* Pellicularia filamentosa *and* P. praticola

Medium I	Medium II*	Medium III	Medium IV
Glucose, 2 g.	Glucose, 2 g.	Glucose, 40 g.	Glucose, 20 g.
$(NH_4)_3PO_4$, 1 g.	Asparagin, 2 g.	Asparagin, 6 g.	Potato decoction†
K_3PO_4, 1·25 g.	K_3PO_4, 1·25 g.	K_3PO_4, 1·25 g.	Agar, 20 g.
$MgSO_4$, 0·75 g.	$MgSO_4$, 0·75 g.	$MgSO_4$, 0·75 g.	
Agar, 20 g.	Agar, 20 g.	Agar, 20 g.	
Water, 1 l.	Water, 1 l.	Water, 1 l.	

* Brown's glucose-asparagin medium.
† 200 g. sliced potato at 80° C. for 30 min. in 1 l. water, filtered and made up to 1 l.

Media I and II proved of no use in comparing cultural characters, as all isolates grew poorly on these media with a thin, sparse mycelium lacking any comparative features. Media III and IV, particularly the latter, proved most useful in developing characters which differed for different isolates.

Isolates of *P. praticola* were uniform in cultural and morphological characters and were readily distinguished from all isolates of *P. filamentosa* after 3 or 4 days' incubation at 25° C. The distinguishing features were faster growth rate (0·56 mm./hr. compared with 0·33 mm./hr.), smaller hyphal diameter in the main 'running' hyphae (6·0–9·6μ compared with 6·9–12·5μ), and particularly the rapid development of a flat, dense, mealy, greyish white and often convoluted surface mat of hyphae, compared with the felty and cottony brown growth of *P. filamentosa*. The only variation observed among these isolates was that, in about half of them, the hyphae immediately above the surface mat developed a cinnamon brown colour after 7–10 days, while the others remained greyish white. There were no cultures among the *P. filamentosa* group which could be confused with these when grown on media III and IV.

All *P. filamentosa* isolates, except the composite strain (isolates 31–36), which grew poorly on medium III, grew profusely on media III and IV, and particularly on medium IV, revealed marked differences in characters similar to those described by Kernkamp *et al.* (1952). These included differences in the optimum temperature for growth, and in hyphal diameter, colour of mycelial mat, presence or absence of zonation, type, distribution and abundance of sclerotia, rate of growth and ability to

form sectors. Additional characters not previously described were the variation in ability to grow from hyphal tips cut off from the parent hyphae, and the type of hyphal extension and branching in the first 24 hr. growth of the tips. Ability to grow varied from normal hyphal extension rate, similar to that in the parent culture, to a complete failure to grow, in some isolates. Type of growth varied from immediate growth in a straight line to a resting period of 24 hr., followed by a further 24 hr. period in which the hyphae grew but curled back and anastomosed freely, forming a 'rosette' before growing out with straight running hyphae characteristic of the usual colony growth.

Analysis of these differences in relation to pathogenicity revealed no correlation, as the isolates within any one pathogenic strain showed as much variation as that between the different strains.

Three other lines of study yielded supporting evidence along these lines. Fifty single-basidiospore cultures were obtained from an isolate of each of four pathogenic strains, 16, 57, 69 and 80. Two of these isolates from 69 (pathogenic to cabbage) were non-pathogenic; the remaining 198 were identical in pathogenicity with their respective parents. When cultured on media III and IV, each group of fifty isolates showed as wide a variation in the characters described above as did the whole range of isolates from the different pathogenic strains. The variation shown in the fifty single-spore cultures from isolate 16 is shown in Pl. 4, fig. 3.

The second line of evidence came from a study of isolates 59 and 62 which on media III and IV readily developed sectors. Hyphal-tip cultures were secured from twenty sectors from each of the parents and grown on media III and IV. These showed as wide a variation in some cultural characters as did different pathogenic strains, but in pathogenicity tests they were identical with the parent isolates.

The third line of evidence was the study of anastomoses between isolates from different pathogenic strains. New combinations obtained by this technique frequently resembled one parent closely in cultural characters, yet in pathogenicity were identical with or closely similar to the other parent.

Thus there would appear to be no essential correlation between pathogenicity and cultural or morphological characters when grown on the four media described.

Cultural comparison of isolates in each soil

Although there appeared to be no correlation between pathogenicity and cultural characters in the general studies referred to above, it was apparent that, if the isolates from any one of the five soils were compared as a group, those belonging to the same pathogenic strain were identical in cultural characters; for example, the isolates from Slough pathogenic to cabbage were identical in culture and easily distinguished from those pathogenic to lettuce, which among themselves were, with one exception, identical. This correlation held true only within each soil: isolates of the same pathogenicity type from different soils differed as much in culture as isolates of different pathogenicity type from the same soil.

Among the forty-one isolates of *P. filamentosa* from the five soils, there were only four which did not show this type of correlation between pathogenicity and cultural characters. These were isolate 36 from Slough, pathogenic to lettuce, which was different from the other Slough isolates of the same strain; isolates 25 and 30 from Norfolk, pathogenic to cabbage and to roots respectively, each of which in culture showed the appearance proper to the other strain, and isolate 20 from Cungena, pathogenic to cabbage, which in culture was similar to the root strain.

Discussion

The results of pathogenicity tests agree with those of previous workers in that the species *P. filamentosa* consists of a wide range of pathogenic strains varying from those specific to one host family to those which can attack a wide range of families; yet other strains appear to be non-parasitic. Tests with the strain pathogenic to Cruciferae on different representatives of this family revealed no specialization within the family, but the work of Kernkamp *et al.* (1952) suggests that specialization even to different varieties of the one plant (potato) is possible. Detailed studies of the nature of pathogenic specialization will be described in a following paper, but until its nature is better understood there seems little value in separating different strains into formae speciales. For example, a number of isolates described above were pathogenic only to Cruciferae or to Solanaceae, but isolates 47 and 62 were pathogenic to both these host families, indicating that these pathogenic capabilities are not mutually exclusive within the one isolate. Further studies using anastomoses and basidiospore development to combine or segregate these capabilities are in progress.

P. praticola appears to be unspecialized, attacking a wide range of hosts at temperatures above 18° C. but below this temperature it attacked only beet. The reason for this temperature effect is not understood.

As far as we are aware, this is the first time an attempt has been made to study the range of *P. filamentosa* strains existing in a particular soil. Although it is unlikely that the complete range of strains, particularly non-pathogenic ones, was isolated, yet the results show that *P. praticola* and one or more strains of *P. filamentosa* often occur together in a soil. In four of the five soils examined a strain (or strains) pathogenic to the commonly grown cultivated plant was isolated. This association might readily be expected. An unexpected result was the occurrence of a strain specific to crucifers in each soil, and apparently at a fairly high population level, judged by the number of seedlings attacked by this strain in making the original isolations. The presence of this strain in soils, such as the Cungena one, where cruciferous crops are never grown may indicate its carry over on cruciferous weeds, but if so it is difficult to explain why occasional isolates of a strain pathogenic to Compositae or Solanaceae were not obtained from these soils, as there is a common population of weeds belonging to these families.

The general cultural comparison of isolates showed that *P. praticola* could be readily distinguished on cultural and physiological characters from the isolates of *P. filamentosa*, but among the latter isolates there appeared

to be no features which could consistently be used to distinguish between pathogenic strains. This is not surprising, as growth on synthetic media must reflect not only the physiological features governing pathogenicity but also those governing its ability to survive as a saprophyte in competition with other members of the soil population. It is likely that these latter factors vary for different soils, and therefore isolates with the same pathogenicity obtained from different soils could reasonably be expected to differ in their growth on synthetic media. Within any one soil, isolates of the same pathogenic strain, with few exceptions, appeared to be uniform in culture and readily distinguished from other strains from the same soil. As saltation, anastomosing and single basidiospore studies have shown that a wide range of cultural types with the same pathogenicity can be obtained from one or two parents, this uniformity suggests that either these mechanisms leading to variation rarely operate under natural conditions, or the variants fail to survive because they cannot compete satisfactorily with the other members of the soil microflora. That factors preventing survival can operate strongly in a soil is indicated by a field trial in which an isolate 18, from Cungena soil, when inoculated at a heavy rate into a field at the Waite Institute in the presence of a suitable host (which it attacked), failed to survive from one season to the next.

The existence of a strain specific to cruciferous plants apparently in fairly high population in all five soils investigated, even where no crucifer crop is regularly grown, suggests that this strain must be a particularly successful competitor in its saprophytic existence, but why this should be correlated with pathogenicity to crucifers is not known.

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EXPLANATION OF PLATE 4

Fig. 1. Effect of *Pellicularia filamentosa* on plant size and root development in wheat. From left to right: control, plants inoculated with isolates 31, 72, 66, and 61.

Fig. 2. Effect of *P. praticola* (isolate 42) on hypocotyls of wheat. Above 18–20° C.

Fig. 3. Variation in culture of a selection from fifty single basidiospore isolates from the root strain isolate 16 of *P. filamentosa*.

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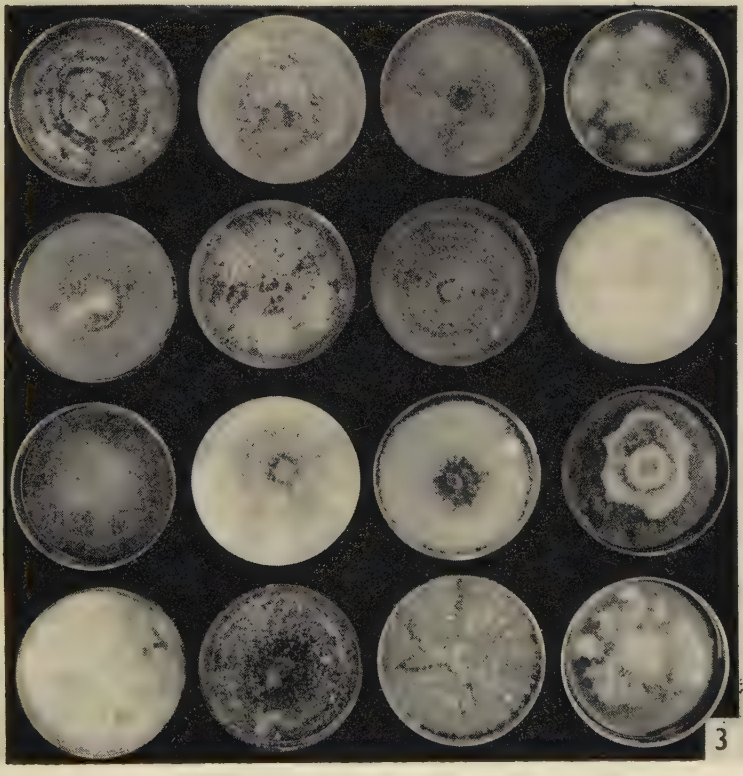

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ZYGOSPORES IN *PIPTOCEPHALIS*

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(With Plate 5 and 1 Text-figure)

Zygospores in *Piptocephalis tieghemiana* and *P. macrospora* have been found to be identical with those of *P. cylindrospora*. The features and development of the zygospores in *P. xenophila* are described. These are formed from buds arising by fusion of the capita of heterogametangia. This species is homothallic. A discussion involves a comparison of zygospores within the genus, the synonymity of *P. cylindrospora*, *P. tieghemiana*, *P. monospora* and *P. macrospora* and some observations on taxonomic criteria within the genus.

Zygospores have been described in *Piptocephalis freseniana* De Bary (1865), *P. tieghemiana* Mat. (1899), and *P. cylindrospora* Bainier (1882), by Brefeld (1872), Matruchot (1899, 1900), and Leadbeater & Mercer (1956), respectively. The latter indicated that, whilst *P. cylindrospora* and *P. tieghemiana* are considered synonymous by Zycha (1935) and Naumov (1939), the considerable disparity in the accounts of the zygospores of those two species disputes this synonymity or the accuracy of Matruchot's account.

Zygospores have now been found in *P. tieghemiana* (from J. L. Yuill) *P. macrospora* (from Baarn) and *P. xenophila* (from Baarn). The last two are species recently erected by Van Beyma (1944) and Dobbs & English (1954), respectively. Dobbs (1954, 1956) considers *P. macrospora* and *P. cylindrospora* as being synonymous.

The zygospores of *P. tieghemiana* and *P. macrospora* are identical with those of *P. cylindrospora* as described by Leadbeater & Mercer (1956). Those of *P. xenophila* show sufficient differences to warrant the account of their structure and development given later.

Zygospore production

Conditions for zygospore formation in the above species have not been critically studied but the following facts are established. In *P. cylindrospora*, *P. tieghemiana* and *P. macrospora*, zygospore formation is a normal occurrence but the best results are obtained by using spore-suspension inocula containing a high proportion of host: parasite spores. The normal procedure, here, is to incubate boiling-tube slopes at 25° C. using potato-dextrose agar and *Circinella? tenella* as host. Zygospores appear, usually, after 2–4 weeks incubation. Different media, different hosts, and incubation within 10–35° C. have no adverse effect on zygospore production. The secret, rather, is where to look for them. These zygospores are found in the agar and, indeed, the mycelial felt can be completely removed and discarded. Careful, sterile, squash preparations of such agar can be used for observing brief stages, only, of development.

Little is known of the conditions required for zygospore production in *Piptocephalis xenophila*. They were first found in 6-month-old cultures which had been allowed to age at room temperature for the express purpose of obtaining zygospores. *Circinella? tenella* and *Penicillium waksmani* on potato-dextrose agar were the different hosts involved. Conversely, these zygospores are not found in the agar but in the mycelial felt since they arise from a short, dense, secondary aerial mycelium. The richest source of zygospores occurred in the mycelial felt overlying the agar, which, by drying, had retracted from the sides of the culture tubes. Cultures were therefore incubated at 25° C. until a good growth of host and parasite obtained and then at 35° C., in order to speed up such a retraction. This method has proved to be a hit-and-miss technique but has provided sufficient fertile material to trace the development of the zygospores.

Zygospores in *Piptocephalis xenophila*

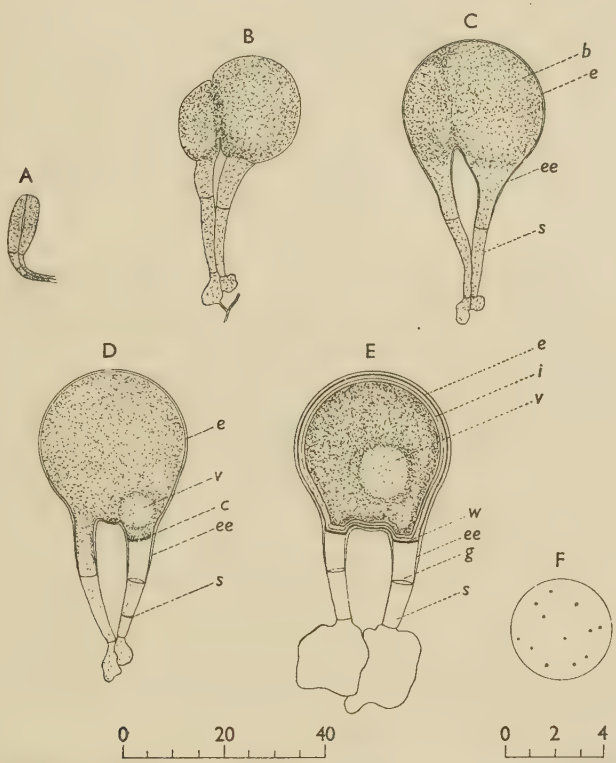
Description. Mature zygospores are spherical or subspherical and are held between pairs of structures which are curved in side view. Each such structure is compounded from a gametangial remnant and a suspensor (Text-fig. 1 E). The stratified exospore possesses an architecture of fine, raised, scattered crinkles and very small scattered pits which only partially penetrate the exospore. The fine outermost layer of the endospore encloses two thick stratified layers of equal width. Exospore extensions reach the cross-walls originally separating the gametangia from the suspensors, but they neither possess the architecture nor the pits typical of the exospore. No appositional thickening is found on the cross-walls delimiting the zygospore.

Such colour as these zygospores possess resides in the innermost endospore layer whose strata become increasingly coloured as they are traced inwards. Normally pale green-yellow, they can present a colour due to the ageing pigments derived from the host. With maturity the suspensors undergo additional septations and exhibit basal hypertrophies which are quite characteristic (Text-fig. 1 E). The zygospores are 24–36μ and in the largest, the walls are 2μ thick.

Development. Fine intramatrical hyphae give rise abruptly to short dense aerial hyphae which are septate, much wider in diameter and irregular in form. Hyphal branches arise in contact, become septate, and the distal cells form copulation branches which later differentiate into hetero-gametangia and suspensors. Copulation branches often arise directly from bulbosities which occur at the abrupt transition from the fine intramatrical mycelia to the secondary aerial hyphae (Text-fig. 1 A, B; Pl. 5, fig. 1). They also appear to arise from the same mycelium and single-spore cultures show this species to be homothallic.

The copulation branches are cylindrical, equal in size, and from early development, in close contact at their tips (Text-fig. 1 A; Pl. 5, fig. 1). The inequality in size appears soon after septation of one or both branches into suspensors and gametangia. This septation occurs when the copulation branches are young and short (Plate 5, fig. 1). Considerable elongation and enlargement follow.

Both gametangia become clavate and finally capitate but not fully so because they are adpressed (Text-fig. 1 B). There is now a considerable disparity in size, the larger gametangium being broadly and the smaller narrowly capitate. The gametangial diameters are now in the approximate ratio of 2:1. Fusion, commencing at the apical portion of contact (Text-fig. 1 B; Pl. 5, fig. 2), is followed by a rounding off and some general



Text-fig. 1. *Piptocephalis xenophila*. A–E, stages in zygospore formation. A, copulation branches from secondary aerial hyphae; B, fusing heterogametangia arising near a sharp transition to the intramatrical mycelium; C, early zygospore bud; D, commencement of zygospore delimitation; E, mature zygospore with basal hypertrophies in the suspensors; F, an exospore area showing size and distribution of pits. *b*, zygospore bud; *c*, retracted residual protoplasm; *e*, exospore; *ee*, exospore extension; *g*, gametangial remnant; *i*, endospore; *s*, suspensor; *v*, vacuole; *w*, delimiting wall.

enlargement of the fused capitate portions of the gametangia rather than distinct budding (Text-fig. 1 C; Pl. 5, fig. 3). The exospore makes an early architectured appearance, but its tapering cylindrical extensions into the future gametangial remnants are free of exospore pits and crinkles. These extensions reach the septa delimiting gametangia and suspensors. At the confluence of the zygospore bud with the future gametangial remnants, heavier circumferential depositions of exospore are often found and mark the planes of the cross-walls delimiting the zygospore bud. However, the

correlation between these depositions and delimiting walls is certainly not as strict as in the zygospores of *P. cylindrospora*.

Before delimitation of the zygospore bud, there is a retraction of all the protoplasm of the gametangia into the bud (Text-fig. 1 D; Pl. 5, fig. 4). This retraction, and consequently the formation of the separating walls, is rarely simultaneous. Retraction and septation usually lag in the smaller gametangium. The delimiting walls are formed on the surface of the retracted protoplasm. It is suspected, but not confirmed, that the retracted protoplasm may condense in its entirety to form the delimiting walls. The lack of residual protoplasm in the gametangial remnants explains the absence of appositional thickening on delimiting walls. Such thickenings are characteristic in the zygospores of *P. cylindrospora*. Zygospore delimitation is followed immediately by the deposition of the three-layered endospore. Maturity brings about no changes in colour but is marked by extra septation and/or characteristic basal hypertrophies in the suspensors (Text-fig. 1 E).

Zygospore formation in *P. xenophila* is the exception, being of an order of less than 0·2 %. Azygosporic formation is the rule. Double azygospores are as frequent as single azygospores derived from the larger gametangium, whilst single azygospores from the smaller gametangium are less frequent. Only the capita of the gametangia are involved in azygospore formation. Since azygospores are formed at different stages of gametangial enlargement, a very interesting array of azygosporic forms is found (Pl. 5, figs. 7–9). When double azygospore formation is considerably delayed, the contiguous azygospores do not truly reflect the heterogametangial conditions (Pl. 5, fig. 7), so obviously demonstrated in other double azygospores (Pl. 5, fig. 8) and in normal zygospore formation (Text-fig. 1 B; Pl. 5, fig. 2). Single azygospores are 15–28 μ. In double azygospores, the larger azygospores are 13–24 μ, the smaller 11–22 μ and the disparity in diameters may be 2·5–10 μ.

Two interesting cases have been met where the gametangia had fused but the zygospores formed from the capita of the larger gametangia (Pl. 5, fig. 6).

Discussion

Zygospores

The structure and development of the zygospores of *P. xenophila* and *P. cylindrospora* offer good agreement. Both are essentially intercalary buds of fused gametangia, but the following differences deserve to be emphasized. In *P. xenophila* the zygospore bud is derived from the fused heads of apposed and capitate heterogametangia. In *P. cylindrospora* curved, clavate and opposed heterogametangia fuse and the zygospore bud results from distinct budding around the point of fusion.

It is interesting to note that two common forms occur in *P. cylindrospora* which are directly related to the degree of curvature of the copulation branches before fusion. Further, a zygospore found in this species had obviously been formed by the fusion of apposed gametangia. Such a variation in form was originally thought to be due to the consistency of the

agar in which they are found (Pl. 5, figs. 10–12). However, rare examples in *P. xenophila* show variations in the degree of apposition of fusing heterogametangia and, consequently, in the form of the mature zygospore. Indeed, one zygospore found had arisen from the fusion of opposed gametangia and agreed in general form with that shown for *P. cylindrospora* in Pl. 5, fig. 11. These variations in form are therefore normal occurrences.

Delimitation of the zygospore bud in *P. xenophila* is preceded by a retraction of the entire protoplasm into it, whilst in *P. cylindrospora* residual protoplasm is isolated in the gametangial remnants by the delimiting walls, on which it condenses to give appositional thickenings.

In *P. xenophila* exospore extensions reach the cross-walls separating the gametangia from the suspensors; in *P. cylindrospora* they are shorter in extent and thicker. The exospore pitting and architecture, so characteristic in both species, are absent from exospore extensions. This arrangement obviously reflects the distinction within the fused heterogametangia of a zygoplasm and a residual protoplasm. Indeed, since in the capitate heterogametangia of *P. xenophila* only the heads are involved in fusion and the formation of the zygospore buds, it is highly probable that protoplasmic differentiation and segregation may occur even in the gametangia. There is, however, the conflicting fact in this species that a retraction of all the protoplasm into the zygospore bud occurs before delimitation. If, as is suspected, the retracted protoplasm condenses in its entirety to form delimiting walls, then protoplasmic segregation is distinct. In *P. cylindrospora* the distinction between a zygoplasm and a residual protoplasm is not only supported by the characters of the exospore but also by the presence of residual protoplasm in the gametangial remnants. It is rather strange why the exospore extensions in this species do not reach the cross-walls separating the suspensors from the gametangia.

Loss in sexuality is excellently demonstrated in *P. xenophila*. This microcephalous species is interesting in that it is the only species of the genus known to extend its range of parasitism to the Ascomycetes, especially to species of *Penicillium*. In fact it grows better on these than on many of the Mucorales. In view of an accepted opinion that parasitism in the latter has a quasi-sexual origin, it is pertinent to record that the type of host does not affect the relative proportion of zygospores to azygospores. It is best perhaps to consider the extension of parasitism by *Piptocephalis xenophila* to the Ascomycetes as a specialization which has been accompanied by a loss in sexuality. *P. xenophila* provides rare instances where the zygospores are formed in the capita of the larger gametangia. From a study of this species alone, such formation must be considered as an expression of loss in sexuality.

Thus two species of *Piptocephalis* agree broadly in the form and development of their zygospores. What is the status of Matruchot's description of the zygospores in *P. tieghemiana*? His account is brief and confusing in that there is no agreement between text and figures. From the latter, it is obvious that the zygospores he described arose from intercalary buds of fusion cells, yet he considered their formation as being identical with 'a Mucor or a Sporodinia'. It is felt that the synonymity of *P. cylindrospora* and *P. tieghemiana* cannot be opposed by Matruchot's description of the

zygospores of the latter. Further, *P. tieghemiana*, here, produces zygospores identical with those of *P. cylindrospora*.

The zygospores of *P. freseniana*, formed from apical buds of fusion cells, provide a formation distinct from that found in *P. xenophila* and *P. cylindrospora*. The zygospores of other species may provide intermediate stages. Neither Brefeld nor Bainier figures the exact delimitation of the zygospore bud, and the reappearance of these zygospores would be interesting.

Taxonomy

The taxonomy of this genus is not entirely satisfactory. The keys of van Tieghem (1875), Zycha (1935), Naumov (1939) and the monographs of Fischer (1892) and Lendner (1908) have used, with varying emphasis, the following main criteria: (*a*) the presence or absence of stolons and rhizoids, (*b*) the form and size of the head cell, (*c*) spore size and shape, (*d*) number of spores per spore chain, (*e*) the presence or absence of striations on sporophores.

The value of spore size in this genus is given by the following instance. In their description of *P. freseniana*, De Bary (1865), Brefeld (1872), Bainier (1907), Vuillemin (1902) all quote different sizes, and Zycha (1935) in his key quotes an addition of his own. Bainier (1907), who also refound the zygospores, is careful to indicate that spore size should not be considered as a critical criterion. Fortunately, the form of the head cell, zygospore features, etc., preserve the integrity of this species.

The following list of synonyms indicates the confusion wrought when spore sizes, spore numbers/spore chain, and the size of the head cell are used, alone, as criteria for erecting species:

Zycha (1935)	Naumov (1939)	Dobbs (1954, 1956)
P. cylindrospora	*P. cylindrospora*	*P. cylindrospora* Bainier, 1882
P. tieghemiana	*P. tieghemiana*	*P. tieghemiana* Mat., 1899
P. monospora		*P. monospora* Mangin, 1899
		P. macrospora Van Beyma, 1944

These 'species' are bound together by the absence of stolons and rhizoids, smooth sporophores (except in *P. macrospora*), spore shape, and spherical head cells. The above authors have all, therefore, accepted the principle that spore and head-cell sizes and the number of spores per spore chain are variable, and, therefore, not exact criteria. Variation in such features obviously reflects the condition of the host-parasite relationship and there is a rough correlation between spore sizes and the number of spores per spore chain. Thus the work of Dobbs & English (1954) on the host range of *P. xenophila* shows that only certain hosts within this range provide an early and successful parasitic growth, and Van Beyma (1944) describing *P. macrospora* states that a sporing rod of 15–20μ forms two or three spores. Dobbs (1954, 1956) has found an overlap of spore and head-cell sizes in *P. cylindrospora* and *P. macrospora*, and concludes that a reduction in such sizes has occurred since *P. macrospora* was first described by Van Beyma (1944). This finding has been confirmed here, whilst *P. cylindrospora* and *P. tieghemiana* are morphologically indistinguishable.

As possible additional criteria, an exhaustive study has been made on the development of head cells and the morphology of appressoria and haustoria. No significant difference is portrayed in the three species concerned.

The principle accepted by the above authors in grouping the respective synonyms seems well justified. It is fully confirmed by the discovery of identical zygospores in the three foregoing 'species'. The main morphological criteria available for the taxonomy of this genus must be limited to (*a*) the presence or absence of stolons and rhizoids, (*b*) spore shape, (*c*) form of the head cell, (*d*) the size of the head cell only in so far as it distinguishes microcephalous from macrocephalous species.

The use of sporophore striations as an accessory criterion needs to be re-investigated. Thus, Van Beyma (1944) describes the young sporophores of '*P. macrospora*' as smooth and older sporophores as striated. Mature cultures of *P. cylindrospora*, here, have also shown striated sporophores. It is also interesting to recall Vuillemin's (1887) account of *P. corymbifer*, unfairly dismissed by Naumov (1939) as being inadequate. Vuillemin indicated that the sporophores may or may not be associated with rhizoids. Zycha (1935) makes it a synonym of the rhizoidal species *P. repens* Van Tieghem & La Monnier, 1873.

The value of the head cell must also be considered as limited. In an unnamed species available here, it is extremely labile. Under standard conditions and on each of several hosts, it shows a size range of 5–20μ diameter. This size variation is accompanied by form variation. The small head cells are solid, obconical with terminal lobes; the large ones are highly dichotomized and a graded series of intermediate forms occurs between these extremes. In fact, this range in form and size embraces descriptions given for the head cells of *P. freseniana*, *P. repens*, *P. arrhiza*, *P. cruciata*, *P. corymbifer* and *P. lemonnierana*. It is also interesting to record that in this species, white unstable mutants occur which are more amorphic than the normal forms.

Thus, zygospores must prove an important supplementary taxonomic criterion and where there are no diagnostic morphological features they may be a primary criterion for speciation.

The synonymity of *P. cylindrospora*, *P. tieghemiana* and *P. macrospora* simplifies the taxonomy of the genus. Zycha's (1935) key is critical and that of Naumov, preoccupied with spore sizes, spore numbers per chain and head-cell sizes is too liberal, except in the case of *P. corymbifer*. Both attack the position of *P. monospora* differently. Mangin (1899) erected this species from a re-examination of pickled material previously used for his studies on the cell wall. At what developmental stage the material was preserved is unknown and Mangin, himself, admitted that it might be a synonym of *P. tieghemiana*. Zycha (1935) makes it a synonym of *P. cylindrospora* and *P. tieghemiana*. Naumov (1939) permits it to stand as a separate species. Whilst the inclusion of *P. monospora* as a possible species within the genus is open to criticism, it seems best, in view of all the foregoing, to follow Zycha.

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EXPLANATION OF PLATE 5

(Fig. 1, × 1650; Figs. 2–12, × 750.)

Figs. 1–9. *Piptocephalis xenophila.* Fig. 1. Young copulation branches. Fig. 2. Fusing heterogametangia. Fig. 3. Zygospore bud. Fig. 4. Zygospore bud with delimiting wall and commencement of suspensor hypertrophy on the left. Fig. 5. Zygospore (basal hypertrophies out of focus). Fig. 6. Zygospore formed in larger gametangium. Fig. 7. Double azygospore showing only a small disparity in azygospore diameters. Fig. 8. Double azygospore reflecting the heterogametangial condition. Fig. 9. Single azygospore with a collapsed, smaller gametangium.

Figs. 10–12. Zygospore forms in *P. cylindrospora.* Fig. 12. An uncommon form derived by fusion of apposed heterogametangia.

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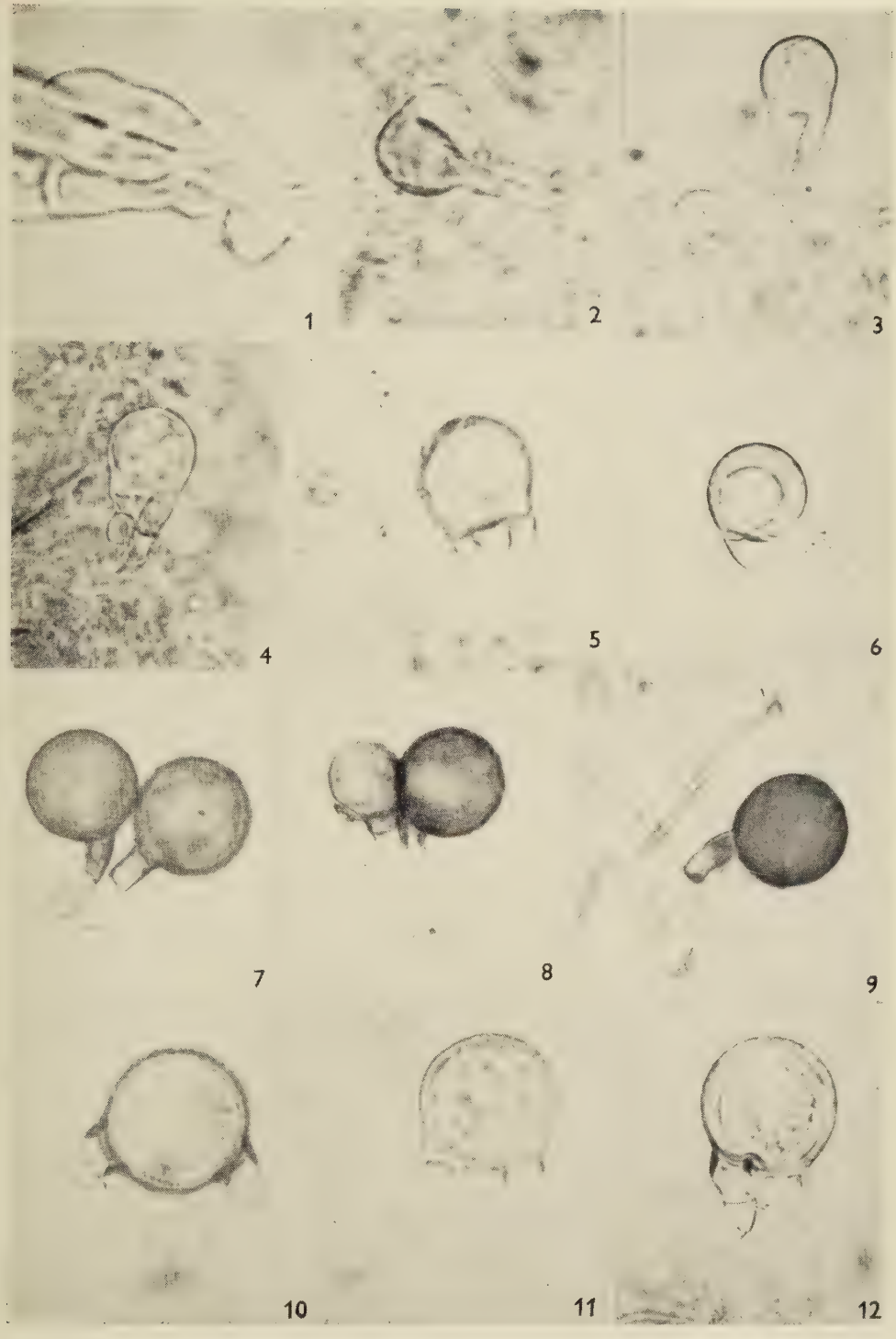

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STUDIES OF BRITISH SPECIES OF *ENDOGONE*

I. MORPHOLOGY AND TAXONOMY

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(With Plate 6 and 3 Text-figures)

Chlamydosporic species. Material of *Endogone macrocarpa* from a number of localities fell into four fairly distinct types; golden-spored, yellow-spored, orange-spored and brown-spored. There was no evidence that these were geographical races or that the variation was due to environmental factors. The species is considered to be a variable one.

Variation in *E. microcarpa* was less marked but relatively large-spored and small-spored variants occurred.

E. fuegiana Speg. is a new record for Britain. The spores of this species are borne in groups at the ends of inflated hyphae. A single fruit-body of an unusual type, in which chlamydospores and sterile vesicles were borne in groups at the ends of a complex system of branched hyphae, was provisionally assigned to the *E. fasciculata–E. vesiculifera* group.

Fruit-bodies of a species associated with mycorrhizal strawberry roots were considered to be chlamydosporic.

A detailed examination of wall-structure in chlamydospores of these species showed that both exospore and endospore are continuous with the corresponding layers of the wall of the subtending hypha.

Zygosporic species. It was confirmed that the size of the zygospores of *E. lactiflua* is correlated with the density of their distribution within the fruit-body. *E. pisiformis*, from the New Forest, is described as the first authentic record of this species in Britain. A fruit-body of *E. microcarpa* contained both typical chlamydospores and zygospores, some of which were of an unusual type. This is the first record of a zygosporic form of this species and only the second record of a mixed zygosporic and chlamydosporic fruit-body in *Endogone*.

Certain problems of the morphology and taxonomy of *Endogone* are discussed and a key to the British species is given.

Introduction

Species of *Endogone* superficially resemble hypogeous Ascomycetes and Basidiomycetes in form and habitat, but differ in mode of fruit-body development. The first record is that of *E. pisiformis* (Link, 1809) and since then the morphology and taxonomy of the genus has been variously interpreted.

The Endogonaceae, as defined by Thaxter (1922), includes four genera: *Endogone* Link, *Glaziella* Berk., *Sclerocystis* Berk. & Br. and *Sphaerocreas* Sacc. & Ellis. The last three have not been found in Britain. They produce fruit-bodies containing chlamydospores, but little is known of their development and life history, and their relationship to *Endogone* remains uncertain (Hawker, 1955).

In *Endogone*, both zygospores and chlamydospores are produced.

Bucholtz (1912) proposed that the genus should be placed in the Mucorales, and this suggestion has been followed by later workers. Previously, however, *Endogone* had been included in the Tuberales by Vittadini (1831) and Tulasne & Tulasne (1851), and in the Hemi-Ascomycetes by Schroeter (1893) and Fischer (1897). The placing of the zygosporic species of *Endogone* in the Mucorales is justified for the time being by the form of the zygospores and the usually aseptate nature of the ground hyphae. The mode of germination of the zygospores has not, however, been observed.

Atkinson (1918) pointed out that the zygosporic species show many affinities with the Ascomycetes and that the conjugation process bears some resemblance to ascus formation in *Dipodascus* and *Eremascus*. If it were demonstrated that the zygospores germinate to form endogenous spores, the position of *Endogone* would more correctly be amongst the Ascomycetes. If, however, germination of the zygospores is followed by the production of a sporangiophore, bearing a sporangium or sporangia, the position of *Endogone* among the Mucorales would be confirmed.

The inclusion of the chlamydosporic and zygosporic forms in one genus was originally proposed because of the similarity in form and habitat. This was justified by Thaxter (1922) who found a North American species, *E. fasciculata*, in which zygospores and chlamydospores were associated in the same spore mass. This was the only species known to produce both types of spore and its discovery was of the greatest importance in establishing the relationship between zygosporic and chlamydosporic forms.

Subsequently Kanouse (1936) demonstrated that chlamydospores were formed in abundance in cultures of the zygosporic species *E. sphagnophila* Atk. and *E. occidentalis* Kanouse. These chlamydospores differed from those typical of *Endogone* in possessing a continuous endospore. In this characteristic they resembled the spores of *Glaziella*. In *Endogone*, the endospore is not continuous and a protoplasmic isthmus is usually left connecting the spore and the parent hypha. A thin exospore covering the endospore has been observed in some species (Thaxter, 1922). The superficial resemblance of the chlamydospores in her cultures to zygospores led Kanouse (1936) to consider the possibility that they might be azygospores. She eventually concluded, however, that they were true chlamydospores.

So-called sporangial forms were also included in the genus *Endogone* by Bucholtz (1912), although they had been referred to the Mortierellaceae by Baccarini (1903). The fruit-bodies are similar in appearance to the zygosporic and chlamydosporic forms but contain thin-walled sporangia. Walker (1923) investigated *E. malleola* Hark. and observed the germination of the sporangiospores. Thaxter (1922) retained the sporangial types in the genus in spite of the absence of a columella in the sporangium. In 1936, however, Kanouse reported that *Mucor*-type sporangia with columellae were formed in cultures of the zygosporic *E. sphagnophila*. She suggested that this type was the characteristic sporangium of *Endogone* and proposed that the sporangial forms, such as *E. malleola*, should be placed in a new genus *Modicella*, in the Mortierellaceae.

Hawker (1954) gave detailed descriptions of three British species (the zygosporic *Endogone lactiflua* and the chlamydosporic *E. microcarpa* and

E. macrocarpa, and mentioned a fourth species which had been found by Mosse (1956) in association with mycorrhizal roots of strawberry. *E. pisiformis* has also been recorded in Britain, but the record is doubtful.

Fruit-bodies of *Endogone* are to be found beneath a variety of trees, within the top one to two inches of humus.

Chlamydosporic species

Endogone macrocarpa (*Tul.*) *Tul.*

Bucholtz (1912) described *E. macrocarpa* and summarized the characters of many collections made in Europe. From his data, it is clear that the diameter of the spores, the thickness of the wall, the width of the supporting hyphae and certain other features, all varied to a considerable extent. The average spore size in any one collection, for example, ranged from 106×92 to $175 \times 159\mu$ and the largest spores were 230μ diam. The thickness of the wall is quoted as $2–14\mu$. The colour of the spores is not often given but 'brown' spores and 'yellowish-brown' ones are mentioned.

Thaxter (1922) described *E. macrocarpa* as being probably the most frequently observed and variable member of the genus. He drew attention to the wide range of spore size, the varying thickness of the spore wall and the presence or absence of radial canals in the wall. Describing a collection of specimens taken from pots of greenhouse soil, he observed that a peridium was not developed on the surface of the fruit-bodies and regarded this as an unusual feature which might have been the result of constant watering.

Neither Bucholtz nor Thaxter gives detailed descriptions of the fruit-bodies or attempts to define any particular types amongst the numerous variations. Thaxter remarks, however, that the variations may prove too great to justify the inclusion in a single species of all the different forms.

Between October 1953 and June 1955 a number of fruit-bodies have been collected in the Bristol area. These were scarce in the dry summer of 1955.

All but a few of the fruit-bodies fell into one of four well-defined types, namely (i) golden-spored, (ii) yellow-spored, (iii) brown-spored and (iv) orange-spored.

The more obvious characters of the various types are summarized in Table 1. A more detailed description has been given by Godfrey (1956).

All four types of fruit-body occurred in the same area at Goblin Coombe, Cleeve, Somerset. Types (i) and (iv) occurred also at Blaise Castle, Bristol, type (i) at Abbot's Leigh, Bristol, type (ii) at Brockley Coombe, Somerset, type (iii) at Failand, Somerset and type (iv) at Wotton-under-Edge, Glos. There is thus no evidence that these are local races.

While the majority of specimens examined fall readily into these four groups on the basis of peridial and other characters, the existence of intermediate specimens shows that a subdivision of the species is not justified. *E. macrocarpa* must, in the present state of our knowledge, be considered to be a variable species which includes a number of overlapping strains. The extent to which this variation is due to environmental factors can only be

Table 1. *Characters of four well-defined types of fruit-body attributed to* Endogone macrocarpa

Type	Surface of fruit-body	Spore colour	Thickness of spore wall (μ)	Approx. diameter of spores (μ)	Wall of parent hypha	Parasitism
(i) Golden-spored	Erect branched hyphae bearing spores	Golden yellow to golden brown *(Primuline Yellow to Ochraceous Tawny)	4–6	130–160	Thickened	Rare
(ii) Yellow-spored	Flattened covering of undifferentiated hyphae	Greenish yellow to brownish yellow (Chalcedony Yellow, Strontion Yellow to Aniline Yellow)	7–10	130–160	Thickened	Present
(iii) Brown-spored	Well-differentiated brownish hairs forming more or less developed peridium	Fawn (Dark Olive Buff to Buffy Brown)	10	180–200	Unthickened	Absent
(iv) Orange-spored	Well-differentiated yellowish hairs forming more or less developed peridium	Yellow to orange (Primuline Yellow, Yellow Ochre to Buckthorn Brown)	4–5	133–175	Unthickened	Absent

* Colours in parentheses are from Ridgway (1912).

decided by the collection of more specimens in other localities. The study of specimens of all types from Goblin Coombe, however, suggests that the variation is not clearly correlated with environmental factors.

Material from Denmark, kindly supplied by Dr M. Lange, did not exactly resemble any of the British specimens but was nearest to the orange-spored type (see Lange & Lund, 1954).

Endogone microcarpa (*Tul.*) *Tul.*

The chlamydosporic fruit-bodies of this species are very constant in form and show less variation than does *E. macrocarpa*. Thaxter (1922) pointed out that the rather constant maximum spore diameter of 48μ distinguishes *E. macrocarpa* from *E. microcarpa*.

Hawker (1954) collected large numbers of fruit-bodies of *E. microcarpa* in the Bristol area and elsewhere, and the writer has made numerous collections during 1953 and 1954 in the Bristol area. It is of interest that Hawker's collections were made during the same seasons in which fruit-bodies of *E. macrocarpa* were scarce and often from areas which later yielded large collections of the latter species. One must conclude that the conditions favouring fruit-body production in the two species are different.

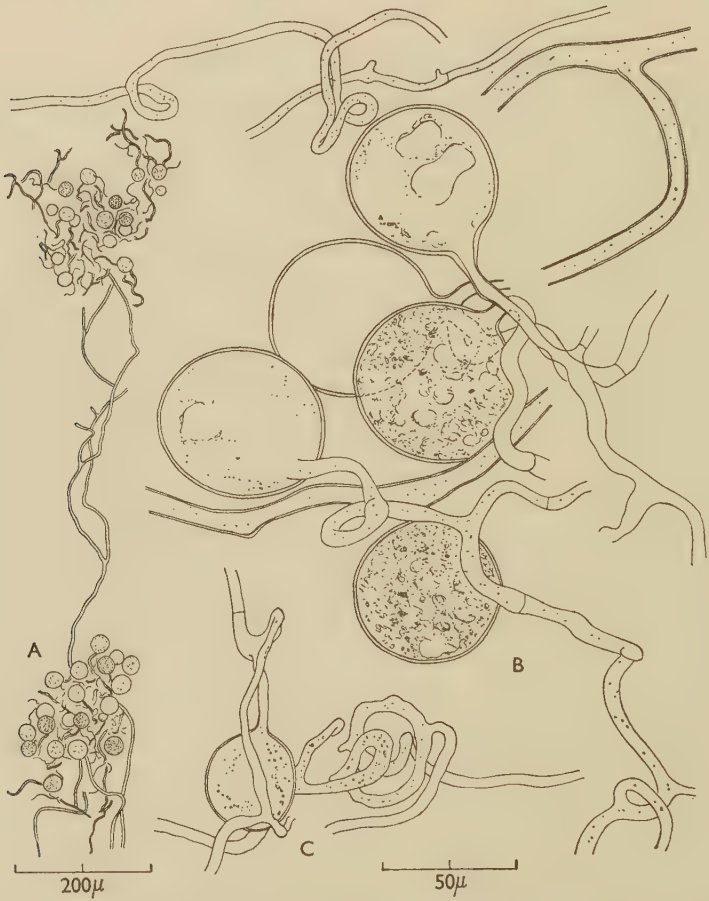
Most of the writer's collections show characters agreeing with Hawker's (1954) description of *E. microcarpa*. Detailed measurements of spore size, however, revealed that fruit-bodies with smaller spores (av. diam. 36μ seldom above 38μ) and others with larger ones (seldom less than 38μ diam., average 42μ, occasionally 46μ) are not uncommon. In the large-spored type of fruit-body there is always a high proportion of thin-walled spores and where these larger spores are thick-walled the channel connecting the spore with the parent hypha is often completely closed. These variations are much less well defined than those described above for *E. macrocarpa*. As with that species, however, there is no evidence that they are peculiar to particular localities or that they arise purely as the result of differing environmental factors. They must be regarded as strain differences which certainly do not justify splitting the species.

Some of the fruit-bodies of *E. microcarpa* collected during the past two years have been associated with tufts of white mycelium. The mycelium consists of loosely tangled hyphae on which solitary chlamydospores are borne (Text-fig. 1). These loose hyphae and chlamydospores were most noticeable in material collected at the top of a limestone cliff in Goblin Coombe, and at Abbot's Pool, Somerset. At both places the soil was rather more shallow and stony than at other localities where *E. microcarpa* was recorded. Fruit-bodies collected from other sites, particularly those with a deep litter layer, usually showed only a trace of external mycelium and very few extramatrical spores.

The loose hyphae resembled the ground hyphae in fruit-bodies of *E. microcarpa* in their wide-angled and infrequent branching, occasional septa, and somewhat undulating outline. They varied from 1·5 to 10μ diam. The larger ones were thick-walled and sometimes yellowish in colour. Many of the hyphae measured 4–6μ diam. and were hyaline, with light greyish contents. Hyphae about 2–3μ diam. were also abundant and it

was from these that chlamydospores were produced. A noticeable feature of the hyphae was their tendency to form coils or irregular spirals so that a loose tangled mycelium resulted.

Chlamydospores were terminal, rarely intercalary, on the branches of the finer hyphae. They were more or less spherical, about 25μ diam.



Text-fig. 1. *Endogone microcarpa*, extramatrical hyphae and chlamydospores. A, groups of extramatrical chlamydospores connected by long aseptate hyphae; B, part of such a group, showing chlamydospores borne terminally on hyphal branches and resembling those formed in the fruit-bodies. Note characteristic angular branching of hyphae, similar to that seen in fruit-bodies. C, a solitary chlamydospore and a characteristic coiled hypha.

(18–30μ), with a hyaline wall 1μ or less in thickness. Some of the spores appeared to be empty, others had greyish protoplasmic contents. The opening of the spore into the parent hypha was clear and wide and no septa have been observed in the neck region.

The chlamydospores were usually scattered at random amongst the loose hyphae. Occasionally, however, they were grouped into well-defined clusters of twenty or more. The finer hyphae were sometimes aggregated

into loose knots. These aggregations were not the beginnings of fruit-bodies but may have been the forerunners of groups of chlamydospores.

New fruit-bodies, as opposed to groups of extramatrical spores, were sometimes laid down amongst the loose mycelium. In the youngest stage observed, no spores were present, but only a compact mass of large, irregularly swollen hyphae. The hyphae were tightly woven together with the characteristic appearance of ground tissue. In older fruit-bodies, young thin-walled chlamydospores had developed. Small mature fruit-bodies were also found in the loose mycelium. It was customary to find a single large fruit-body with two or three smaller ones in the associated mycelium.

Neither Thaxter (1922) nor Hawker (1954) made mention of chlamydospores formed outside the fruit-body in *Endogone*. Mosse (personal communication) has observed small chlamydospores formed on the mycelium associated with fruit-bodies of an undescribed species of *Endogone* which she has found in association with mycorrhizal strawberry roots (1953).

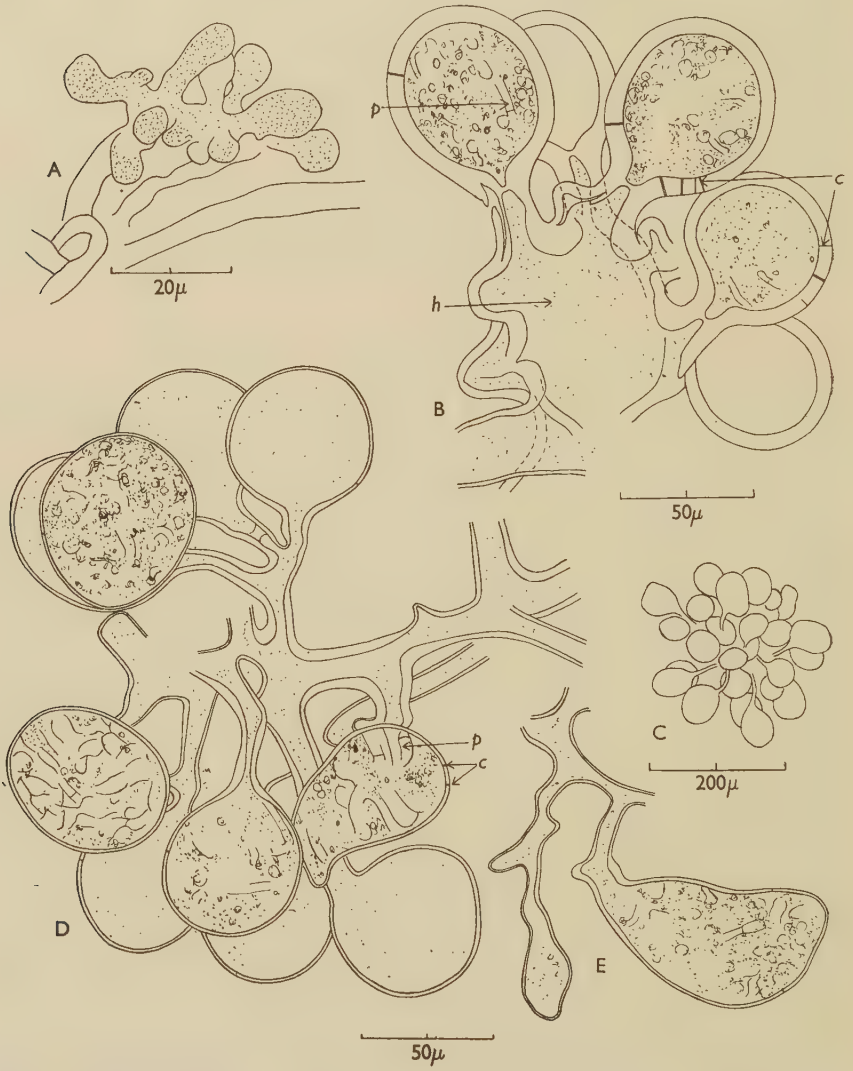
Endogone fuegiana *Speg.*, *Spegazzini* (1887*a*, *b*)

Several mature fruit-bodies and one very young one of a chlamydosporic species, found in a carboniferous limestone area of Somerset, were identified as *E. fuegiana* Speg. from Thaxter's description (1922, p. 310, figs. 33–34). This species has not previously been recorded in Britain.

Fruit-bodies. At first pure white, becoming dirty fawn, small (up to $4{\cdot}5 \times 4 \times 4$ mm.), firm, hard, sometimes lobed or wrinkled, odourless, general appearance as *E. microcarpa*. *Pseudoperidium*. Surface of fruit-body at first covered with delicate erect hairs, about 300μ long, later by a thin pseudoperidium of tangentially arranged hyphae. *Gleba*. At first white or cream, later fawn or greyish fawn, no incorporated foreign matter present (thus resembling *E. microcarpa* rather than *E. macrocarpa*), groups of mature chlamydospores showing up as brown patches visible to the naked eye. Matrical hyphae near surface are branched at right angles, $3{\cdot}5\mu$ diam., often septate and empty, those deeper within fruit-body are 3–$10{\cdot}5\mu$ diam., thin-walled, closely interwoven. *Chlamydospores*. In distinct groups of about ten (Text-fig. 2A, B), produced as buds from an inflated hyphal end, usually separated by ground hyphae. Spores of similar age and wall thickness in any one group but groups of varying age found within same fruit-body, the younger ones usually in outer layers. The hypha bearing a group of spores usually becomes thick-walled and may bear additional small swellings which may be chlamydospore initials which have failed to develop, perhaps owing to overcrowding. Spores usually sessile but occasionally with short stalks, exceptionally with stalks up to 122μ long. Spores typically egg-shaped sometimes laterally compressed when in contact with others of the same group. Average size $76 \times 65\mu$ but within range 30–80μ, (cf. Spegazzini's measurements, for type material, $80 \times 64\mu$). Spore wall at maturity 5–7μ thick, septum sometimes formed at neck by ingrowth of inner layer of endospore. Frequently invaded by fungal parasite.

Habitat and periodicity. Collected from three sites at Goblin Coombe,

Somerset, and also at Wraxall, Somerset, always beneath yew trees, where ground vegetation was sparse or lacking. All these sites also yielded *E. microcarpa*; *E. macrocarpa* was found at all but one of them. Mature and nearly mature specimens collected in October and November; the immature specimen was found in June.



Text-fig. 2. *Endogone fuegiana*. A, group of young chlamydospores. B, mature chlamydospores, note inflated parent hypha (*h*). Radial canals (*c*) in spore walls indicate the presence of a fungal parasite (*p*).

A fruit-body attributed to the *E. fasciculata–E. vesiculifera* group. C, a typical cluster of chlamydospores, teased out of fruit-body. D, mature chlamydospores borne terminally on branches of a hyphal complex. Note much thinner walls than in *E. fuegiana* and presence of radial canals (*c*) and fungal parasite (*p*). E, irregularly shaped vesicles, which may be abnormal chlamydospores.

An unusual fruit-body provisionally referred to the Endogone fasciculata–E. vesiculifera *group of Thaxter* (1922)

Fruit-body, 7 × 4 × 4 mm., firm, brown, old, barely distinguishable from a small lump of earth, much humus incorporated in gleba which thus appeared dark. *Surface of fruit-body.* No trace of pseudoperidium, spores visible at surface, probably owing to age of specimen. *Gleba.* Matrical hyphae obscured by presence of incorporated humus particles, spores apparently uniformly distributed when gleba sectioned but when portions were teased out they were seen to be attached in grape-like clusters (Text-fig. 2 C, D). *Chlamydospores and vesicles.* In groups consisting of typical chlamydospores, borne terminally on short branches arising from a complex of interwoven hyphae, and irregularly shaped vesicles (Text-fig. 2 E) which did not form a continuous margin to group (in contrast to *E. vesiculifera* Thaxter (1922)). Chlamydospores more or less spherical, av. diam. 55μ, wall commonly 2μ thick, occasionally up to 3·5μ, dull yellow (Ridgway, Mustard Yellow or Old Gold to Mars Yellow). Endospore continuous with thick wall of parent hypha, septum usually not present at neck of spore. Some spores were oval or irregular in shape and intermediate between the typical spherical chlamydospores and irregularly shaped vesicles. Vesicles, 60–85 × 20–40μ, thin-walled or with thick (2μ) yellow wall resembling that of typical chlamydospore. Both spores and vesicles were empty or parasitized.

Habitat. In humus layer under yew tree. *E. macrocarpa* also present. Collected June 1955.

Probable affinities. The grouping of the chlamydospores on separate tangles of hyphae suggests a relationship with *E. fasciculata.* Thaxter and *E. vesiculifera* Thaxter (Thaxter, 1922). The absence of zygospores does not necessarily exclude the present species from *E. fasciculata*, as Thaxter pointed out that these were not 'invariably associated with the chlamydosporic form'. The presence of irregular vesicles, however, suggests a closer affinity with *E. vesiculifera.* The form, size and arrangement of the vesicles in the present specimen does not agree closely with those of *E. vesiculifera.* It is possible to trace a complete series from typical spherical chlamydospores to irregular shaped vesicles, which suggests that the latter are aborted or otherwise abnormal spores. While Thaxter considered that the distinctive vesicles in his material were probably the homologues of the spores, he did not see any intermediate forms. The chlamydospores in the present specimen were rather smaller than those of Thaxter's material of either *E. fasciculata* or *E. vesiculifera.* The walls are thinner than those of the type material of *E. fasciculata* or those figured by Thaxter for *E. vesiculifera*, but such a difference is within the range of variation, described by the present writer for the species *E. macrocarpa.* This difference cannot be ascribed to immaturity of the Somerset material since it was obviously a very old fruit-body.

Until more specimens are collected it is not possible to determine whether the specimen is best classified as *E. fasciculata*, *E. vesiculifera* or as a distinct but rather closely related species.

A species of Endogone *associated with mycorrhizal strawberry roots*

Mosse (1953, 1954*a*) described an unnamed species of *Endogone* in association with mycorrhizal roots of strawberry. Later (Mosse, 1954*b*) she stated that the fruit-bodies, which are 1 mm. or less in diameter, 'consist of a loose weft of irregularly septate, dichotomously branched hyphae in which a variable number of thick-walled zygospores (1–16) and immature thin-walled spores are irregularly embedded'.

Hawker (1954), having examined some of the fruit-bodies, describes them as containing thick-walled yellow chlamydospores. Through the kindness of Miss Mosse, the writer examined similar material and confirmed Hawker's interpretation of the spores as chlamydospores.

The spores are spherical or oval in shape and often very large (up to $252 \times 224 \mu$). In general structure they are similar to the chlamydospores of *E. macrocarpa* and other chlamydosporic species. The yellow endospore is about $3–5 \mu$ in width and the thickening is continued into the parent hypha. The thin hyaline exospore, covering the yellow wall, is sometimes quite prominent and it may even be torn away from the spore. The opening of the parent hypha into the spore is typically unoccluded, but a thin septum is sometimes present in the neck region. This septum may be incomplete and faint, and apparently develops as an outgrowth of the hyphal wall. It is thus comparable with the septa occurring elsewhere in the matrical hyphae, and bears no resemblance to the endospore of a zygospore. There is never more than a single hypha subtending the spore, although the parent hypha may be branched in a manner which at first sight might suggest two gametangia. Mosse's figures (1954*a*, fig. 29; 1956, fig. 3) not only do not suggest that the subtending hyphae could be interpreted as gametangia but are actually in agreement with the interpretation given above.

This species resembles *E. microcarpa* in the production of extramatrical mycelium bearing chlamydospores, which are thin-walled and smaller ($40–55 \mu$ diam.) than those in the fruit-bodies.

A short account of germination of the spores from fruit-bodies is given by Mosse (1954*a*) and from this and personal communications from her it is clear that the type of germination is exactly comparable to that described by Godfrey (1955) for *E. microcarpa* and *E. macrocarpa*, of which a fuller account is in preparation. This provides additional evidence of the chlamydosporic nature of these spores.

Structure of the chlamydospore wall

There is some uncertainty in the literature about the structure of the chlamydospore wall. Thaxter (1922) mentions a thin hyaline exospore surrounding the thick endospore wall in some species, e.g. *E. tenebrosa* and *E. canadensis*. In *E. radiata* there is said to be no visible distinction between exospore and endospore, and an exospore is not particularly mentioned in the remaining species.

In his illustration of *E. tenebrosa* the course of the exospore is not made clear, although it is shown in the neck region of the spore.

Bucholtz (1912) illustrates chlamydospores of *E. macrocarpa* and *E. microcarpa*. In some the exospore is shown as being continuous with the hyphal wall, while the endospore extends only to the neck of the spore. In others, the endospore is continuous with the hypha and the exospore apparently comes to an end.

The illustration given by Lange & Lund (1954, fig. 1*c*) of the junction of hypha and spore in *E. macrocarpa* is difficult to interpret, but suggests that the thickened part of the endospore ends at the junction of the spore with the parent hypha.

Observations made on the British material lead to the conclusion that the chlamydospores from fruit-bodies of all the species are similar in their structure. An endospore and a thin exospore are present, and both are continuous with the hyphal wall. The *thickening* of the endospore, however, ends at, or just below, the junction of spore and subtending hypha. It must be emphasized that great variation exists between individual chlamydospores from the same fruit-body and between those of different fruit-bodies of the same species. The exospore can scarcely be discerned in some cases, but in others is quite distinct.

Exospore. The exospore is a thin hyaline membrane which forms the outer covering of the spore and is continuous with a similar covering of the hyphae. As a rule it is closely adherent to the endospore and only separates from it when, for example, the spore becomes dry and the wall cracks. The exospore readily takes up stains, such as aniline blue, which leave the endospore unaffected. In fruit-bodies of *E. macrocarpa* which contain a lot of incorporated humus, the spore wall may be obscured by adherent debris and the exospore may not be visible. It seems likely that it becomes broken and roughened so that the humus particles adhere to it. The exospore is sometimes visible in the neck region, even when it is obscured elsewhere.

Endospore. The endospore is the prominent part of the spore wall and forms a thick brown or yellowish layer. Malençon (1947) observed an unusual division of the endospore into two layers, in *E. microcarpa*. The inner layer (which occupied about half the total width of the endospore) had a greater affinity for stains than the outer one.

During the present study a similar division of the endospore into two layers has sometimes been observed in *E. microcarpa*, *E. macrocarpa* and *E. fuegiana*. The inner layer is less smooth and homogeneous than the outer layer but there is little difference in colour. In the majority of spores, no such marked division of the endospore is visible, but the innermost region of the endospore (about 1 μ in width) is usually more refractive than the outer part. It may appear to be a distinct layer, but is actually no more than a part of the endospore and does not constitute a separate stratum.

The endospore is continuous with a similar lining of the parent hypha. Refraction and other optical difficulties make it hard to trace the course of the inner and outer layers of the endospore into the hyphal wall. It seems, however, that the inner layer is continuous with the inner wall of the hyphae. In some species the parent hypha is thickened for some distance below the spore, and in that case the material of the outer, homogeneous part of the endospore is also continued into the parent hypha, but comes to an end at a distance of 50–200 μ below the spore.

Fine radial canals sometimes traverse the spore wall at many points and small, conical projections inwards from the endospore may also be observed. The projections are formed of material similar to that of the inner layer of the endospore. These features are invariably associated with parasitic infection of the fruit-bodies and will be more fully described in a later paper.

Zygosporic species

Endogone lactiflua *Berk.*

This species, first described by Berkeley (1860), is common in Britain. Hawker (1954) gave a detailed description of the morphology and development of the fruit-bodies.

The present writer has re-examined Hawker's material and has made numerous other collections in the Bristol area. No correlation between spore size and any obvious environmental factor, such as the species of tree beneath which the fruit bodies were found, could be demonstrated. Specimens with spores of markedly different sizes were sometimes found adjacent to one another. Hawker's suggestion that spore size was correlated with density of spore distribution was confirmed.

An abnormal fruit-body (collected by Dr L. E. Hawker in the New Forest in September, 1954) had a few small, colourless, thin-walled vesicles, of 8–40μ diam. among the ground tissue of the gleba. Fine hyphae, which may have been those of a parasite were found among the hyphae of the gleba and had penetrated some of the spores but these had no connexion with the vesicles. Since no similar specimen has been found it is not possible to decide whether the vesicles were immature chlamydospores of *E. lactiflua* or were a stage in the life-history of an unidentified parasite.

Endogone pisiformis *Link*

A zygosporic fruit-body collected by Dr J. Fraymouth in the New Forest in September 1954 was identified as *E. pisiformis* Link from the description given by Thaxter (1922).

There is some doubt as to whether *E. pisiformis* has been found in Britain before. Hawker (1954), from an examination of herbarium specimens, pointed out that all available recorded specimens of *E. pisiformis* were *E. macrocarpa* or *E. microcarpa* and she concluded that *E. pisiformis* was a doubtful record. She was unable to trace a specimen collected by Bucknall (1882) from the Bristol area. *E. microcarpa* is relatively common in the district, however, and it seems likely that Bucknall made a wrong identification.

Habitat. In humus beneath beech, in contrast to the American specimens which, according to Thaxter, were rarely found below the leaf cover, but were usually attached to mosses, twigs, etc.

Fruit-body. 3 mm. diam., rounded, firm, waxy, pale yellow. The gleba was also pale yellow. *Surface of fruit-body* was covered by branched, thick-walled, hyaline hairs, about 4μ diam., with the branches tapering to fine points. A thin, tough pseudoperidium was formed by the firmly woven

bases of these hairs. *Gleba.* The hyphae in the interior of the fruit-body measured 2–8μ diam., but were often swollen in an irregular manner. They were thin-walled and collapsible. The gleba was fairly soft in texture and contained densely packed zygospores with no trace of a surrounding hyphal sheath. The spores were at a fairly uniform stage of development, most of them having a definite endospore, but possibly not fully mature. *Zygospores.* Thaxter gives the dimensions of the spores as 35–60 × 30–45μ, but those in the British material were larger. The spores were usually ellipsoidal (76–80 × 60–68μ), but sometimes spherical (av. diam. 73μ). Under low magnification the spores were light brown, but under high magnification the exospore appeared greenish buff (Ridgway, Deep Olive Buff), and the endospore more or less hyaline. Refraction tended to mask the true coloration. *Development of zygospores.* The zygospores were formed as a thin-walled vesicle above the point of contact of the subequal gametangia. In older spores the wall of the vesicle or exospore was 3·5–4·5μ thick and buff in colour with a hyaline endospore, about 3μ thick, laid down within the exospore, closing the entrance to the gametangia. The gametangial walls remained unthickened (Text-fig. 3D, E).

In the younger spores, the contents had the appearance of numerous very small granules and droplets. In older ones, the granules were well-defined and about 1·5μ diam.

A zygosporic form of Endogone microcarpa

In September 1954, a fruit-body was found at Goblin Coombe, Somerset, which contained both typical chlamydospores and zygospores.

Thaxter (1922) described *E. fasciculata* as being the only form in which zygospores and chlamydospores had been found in the same fruit-body. He stated that zygospores did not seem to be invariably associated with the chlamydosporic form.

Dowding (1955) referred to both *E. fasciculata* and *E. sphagnophila* Atk. as having zygospores and chlamydospores within the same fruit-body, but she gave no authority for the statement with regard to *E. sphagnophila.*

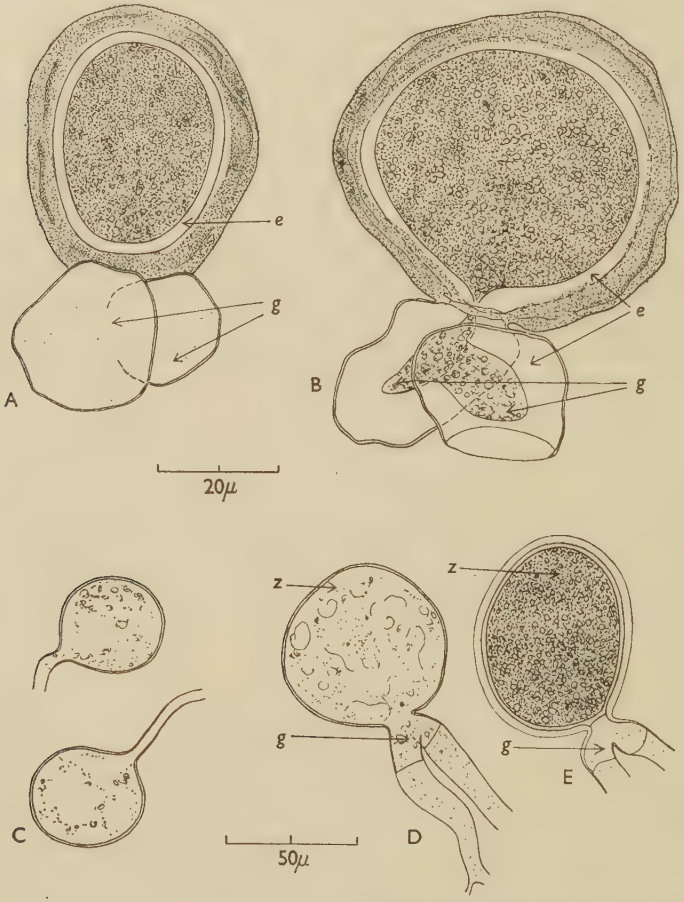
The chlamydospores of the Goblin Coombe specimen showed no significant difference from those of *E. microcarpa.* In macroscopic characters, too, the fruit-body was typical of *E. microcarpa.* It is therefore considered to be a zygosporic form of this species.

The conditions that determine zygospore production remain obscure. The fruit-body was found at a site from which normal chlamydosporic specimens of *E. microcarpa* were collected on several occasions. Among the numerous fruit-bodies of this species examined during the past two years no trace of zygospores has been found in any other specimen.

Habitat. The fruit-body was found in the litter layer beneath yew trees in a habitat typical for *Endogone.* A sparse covering of vegetation was present, including species of *Viola, Fragaria, Pteridium* and *Rubus.*

Fruit-body. The specimen measured 4 × 4 × 5 mm. and was rounded, smooth and whitish fawn in colour. The texture was firm. *Surface of fruit-body.* A thin pseudoperidium about 30μ wide, composed of woven hyphae without chlamydospores, was present. *Gleba.* In section the gleba was

cream-coloured with conspicuous dark orange patches in a ring near the periphery. On examination the orange areas showed scattered zygospores interspersed with chlamydospores. The pale areas contained only chlamydospores. The band of zygospores was about 500μ wide and placed 400μ in from the periphery of the fruit-body. The hyphae in the interior



Text-fig. 3. *Endogone microcarpa*, zygosporic form. A, zygospore dissected out of fruit-body. The two empty gametangia (*g*) remain attached but the suspensor cells have been broken away. Note endospore (*e*) lining the spore. B, zygospore of unusual form in which endospore (*e*) lines both spore and gametangia. The contents of the spore are continuous with those of the lumen of the thick-walled gametangia (*g*). C, chlamydospores from same fruit-body.
E. pisiformis, D, young zygospore (*z*) developing from two equal gametangia (*g*). E, older zygospore (*z*) in which the endospore has sealed off the entrance to the gametangia (*g*).

of the fruit-body were characteristic of the chlamydosporic type of *Endogone*, with right-angled branching and occasional septa (see Hawker, 1954, fig. 2K). They were about 4μ wide (2–7·5μ) but sometimes irregularly swollen. *Zygospores* (Text-fig. 3A, B; Pl. 6). The zygospores were for the most part mature and very conspicuous from their dark golden

brown colour. The gametangia were not readily visible unless the spores were teased out from the fruit-body. The mature spores measured about 50μ diam. (38–67μ) and were more or less spherical or oval in shape.

The gametangia were of unequal size and the zygospore was produced as an outgrowth from the larger one as in *E. lactiflua*. The gametangia were cut off by a septum from the supporting hyphae, which readily broke off at this point and were consequently not often observed.

The wall of the larger gametangium was continuous with the exospore which was thin and tawny-coloured (Ridgway: Yellow Ochre to Raw Sienna). At maturity its surface was sculptured into minute raised dots. It covered the endospore loosely and was often wrinkled, giving the spore an angular appearance. The endospore was smooth and firm, about 6μ wide and of a pale greenish yellow colour.

Many of the zygospores were subtended by colourless thin-walled gametangia, and the cavity of the spore was separated from the cavity of the gametangia by the continuous endospore (Text-fig. 3A). Some of the spores were remarkable, however, in that the endospore was continuous with a thick lining of the gametangia, so that a continuous wall must have been laid down lining both the spore and the united gametangia (Text-fig. 3B). The lumen of the spore was then left in contact with the lumen of the gametangia by a narrow canal in the neck region of the spore but there was no open connexion with the suspensor cells. The original gametangial wall, which was yellow but not appreciably thickened, was quite distinct from the inner lining. Such structures must be considered to be abnormal zygospores. It is unfortunate that neither these nor the normal spherical zygospores could be induced to germinate.

The spore contents had the appearance of spherical granules and droplets. When the gametangia were lined by a wall continuous with the endospore, their protoplasmic contents were similar, but when they remained thin-walled their contents were pale and scarcely visible.

When the spores were teased out from the fruit-body, the gametangia, particularly the thick-walled ones, sometimes remained attached to the spore proper, but sometimes were broken off at the junction of gametangium and spore.

A few immature zygospores were present in the fruit-body, but there were no early stages in conjugation. The immature spores showed only a pale yellow exospore.

Sections of fruit-body were stained with Heidenhein's iron alum haematoxylin to demonstrate the nuclei. In nearly all the zygospores a single large nucleus was present, but occasionally two smaller ones were observed. By analogy with *E. lactiflua*, it is likely that the large nucleus was a fusion nucleus, which would later divide. In *E. lactiflua* the fusion nucleus divides repeatedly while the spore is still immature, and the mature spore is multinucleate (Hawker, 1954).

Chlamydospores. The second type of spore within the fruit-body was a terminal chlamydospore of the *E. microcarpa* type (Text-fig. 3C). The spores were mainly 38–45μ diam. The majority of those in the outer region of the fruit-body and amongst the zygospores were still thin-walled (1–2μ). The more mature ones were concentrated in the central area of the fruit-body;

in these, the wall was 4–5 μ in thickness, pale yellowish green and with the opening of the spore more or less occluded. The chlamydospores are thus typical of the large-spored form of *E. microcarpa*, described on p. 121.

Germination of spores. The fruit-body was kept in moist filter-paper at 10° C. for 6 weeks before it was discovered to be an unusual specimen. There is little possibility of the zygospores having been formed as a result of storage at low temperature, since other fruit-bodies of *E. microcarpa* stored under similar conditions produced no zygospores.

Small portions of the fruit-body were washed and spread on plain agar and incubated at 20° C. The plates were kept for several months but the zygospores did not germinate. The chlamydospores showed about 10 % germination of the type described by Godfrey (1955) for *E. microcarpa*.

Discussion

The genus *Endogone* provides many problems. The present re-examination of the morphology of the British species throws light on at least two of these, namely the structural characters which distinguish chlamydospores from zygospores and the relationship between chlamydosporic and zygosporic forms.

Characters distinguishing chlamydospores from zygospores

The main distinction between chlamydospores and zygospores is that the latter are produced as the result of the conjugation of two gametangia, and are therefore subtended by two hyphae, while the former are produced as terminal enlargements of a single hyphal branch and are thus subtended by only one hypha. This is usually quite clear, but in old zygosporic fruit-bodies the gametangia and suspensor cells may have disintegrated. Moreover, the possibility of the parthenogenetic formation of zygospores from a single gametangium cannot be excluded. Thus it is not always possible to distinguish between the two types of spore by their mode of formation.

Thaxter (1922) pointed out that true zygospores show a continuous endospore cutting them off from the gametangia, while the endospore of a chlamydospore is continuous with the wall of the parent hypha with which the spore is thus in protoplasmic communication. Owing to the narrowing of the communicating canal by the ingrowth of the wall at the junction of the spore with the subtending hypha, it is often difficult to determine whether the endospore is continuous or not. This has led to difficulties of interpretation of chlamydosporic material, as with the unnamed species described by Mosse (1953).

The continuous endospore of true zygospores is relatively easy to demonstrate in *E. lactiflua* or *E. pisiformis* since the mature zygospores are obviously sealed off from the gametangia. The sexually produced spores in the mixed fruit-body of *E. microcarpa* (p. 129) are of two kinds. Those in which the gametangia remain thin-walled and the spore becomes separated from them by the endospore are typical zygospores. In others, however, the endospore is continuous with a thick lining of the gametangia. Here spore and gametangia are separated by this secondary wall from the suspensors

and the spore may be interpreted as differing from a typical zygospore only by the inclusion of the gametangia within the endospore. There is no valid reason why these should not be considered to be true zygospores, though of an unusual form.

Relation between zygosporic and chlamydosporic forms

Thaxter's discovery of *E. fasciculata* fruit-bodies, containing both chlamydospores and zygospores, provided a link between chlamydosporic and zygosporic forms. The question of whether other chlamydosporic species might produce zygospores has remained uncertain.

It is now clear that zygospores may be produced by *E. microcarpa*. The mixed fruit-body of *E. microcarpa* is of particular interest as representing a simpler type than *E. fasciculata*. The chlamydospores are scattered singly throughout the fruit-body and the zygospores, although they are confined to definite areas of the gleba, are not clustered together, as are those of *E. fasciculata*.

Thaxter (1922) suggested that *E. lactiflua* might prove to be the zygosporic stage of *E. macrocarpa*, but Hawker (1954) points out that this is unlikely 'since the characteristic hyphae of *E. macrocarpa* are not seen in *E. lactiflua* while latex is present in the latter and absent in the former'. The discovery of fruit-bodies containing both chlamydospores and zygospores by Thaxter for *E. fasciculata*, by the writer for *E. microcarpa*, and possibly by Dowding (1955) for *E. sphagnophila*, makes it unlikely that purely zygosporic and chlamydosporic fruit-bodies can be looked upon as different stages in the life cycle of a single species. *E. microcarpa* and *E. fasciculata* provide evidence that typically chlamydosporic species may produce zygospores within the same fruit-body. The question naturally arises as to whether chlamydospores are ever found in the typically zygosporic fruit-bodies. No records of such specimens are to be found in the literature. In this connexion, however, attention may be drawn to the unusual fruit-body of *E. lactiflua* (see p. 128) in which vesicles which bore some resemblance to immature chlamydospores were present in an otherwise typical fruit-body.

The discovery of these mixed fruit-bodies also makes it more unlikely that the chlamydospores are azygospores produced by forms which have lost the power of conjugation (as was tentatively suggested by Thaxter (1922) and Hawker (1954) and followed by Lange & Lund (1954)), since even in the normally entirely chlamydosporic *E. microcarpa* zygospores have now been demonstrated in an exceptional fruit-body. The structure of the chlamydospores is also against this interpretation.

The inclusion of chlamydosporic and zygosporic forms within a single genus is obviously justified. Further cultural studies are desirable to determine the nature of the sporangial stage, if any.

Tendency towards increasing complexity as exhibited by British species

A greater diversity of form than was previously recognized has now been found among British species of *Endogone*. Among the chlamydosporic species, those previously recorded (*E. microcarpa*, *E. macrocarpa* and Mosse's unnamed species) bear their chlamydospores singly at the apices of distinct

hyphae or hyphal branches and are scattered throughout the gleba. In the specimen showing affinities with Thaxter's *E. fasciculata–E. vesiculifera* group the spores are borne terminally at the apices of hyphal branches but the subtending hyphae are aggregated in distinct though complex groups which become visible when the gleba is teased out. Vesicles which may be abortive spores are also borne on these hyphal complexes. In *E. fuegiana* the grouping of the spores is visible to the naked eye and they are formed on complex inflated hyphae or sporophores. This is the most complex chlamydosporic fruit-body seen and approaches the arrangement of spores in groups and layers described by Thaxter for other genera of the Endogonaceae.

Among the zygosporic forms *E. lactiflua* shows an advance on the other two species in the development of a separate hyphal sheath around each zygospore.

Key to the British species of *Endogone*

The key to British species of *Endogone*, given by Hawker (1954), provides only for *E. lactiflua*, *E. macrocarpa* and *E. microcarpa*. The discovery of *E. pisiformis*, *E. fuegiana* and a specimen resembling *E. vesiculifera* in Britain makes a new key necessary.

1. Fruit-bodies zygosporic. **2**
   Fruit bodies chlamydosporic or with zygospores and chlamydospores mixed. **3**
2. Zygospores surrounded by a hyphal sheath, gametangia unequal. **E. lactiflua**
   Zygospores without a hyphal sheath, gametangia sub-equal. **E. pisiformis**
3. Chlamydospores not in groups, borne singly on separate hyphae. **4**
   Chlamydospores in groups. **6**
4. Chlamydospores less than 50 μ diam. **E. microcarpa**
   Chlamydospores more than 50 μ diam. and commonly more than 100 μ. **5**
5. Fruit-bodies 2 mm. or more diam. containing numerous spores. **E. macrocarpa**
   Fruit-bodies 1 mm. or less diam. containing less than 40 spores
   Endogone sp. (Mosse, 1953)
6. Chlamydospores in well-defined groups, each group composed of a number of spores almost sessile on an enlarged hyphal termination **E. fuegiana**
   Chlamydospores in poorly defined groups, each group composed of spores borne on short side branches of interlacing thick-walled hyphae
   E. fasciculata-E. vesiculifera group

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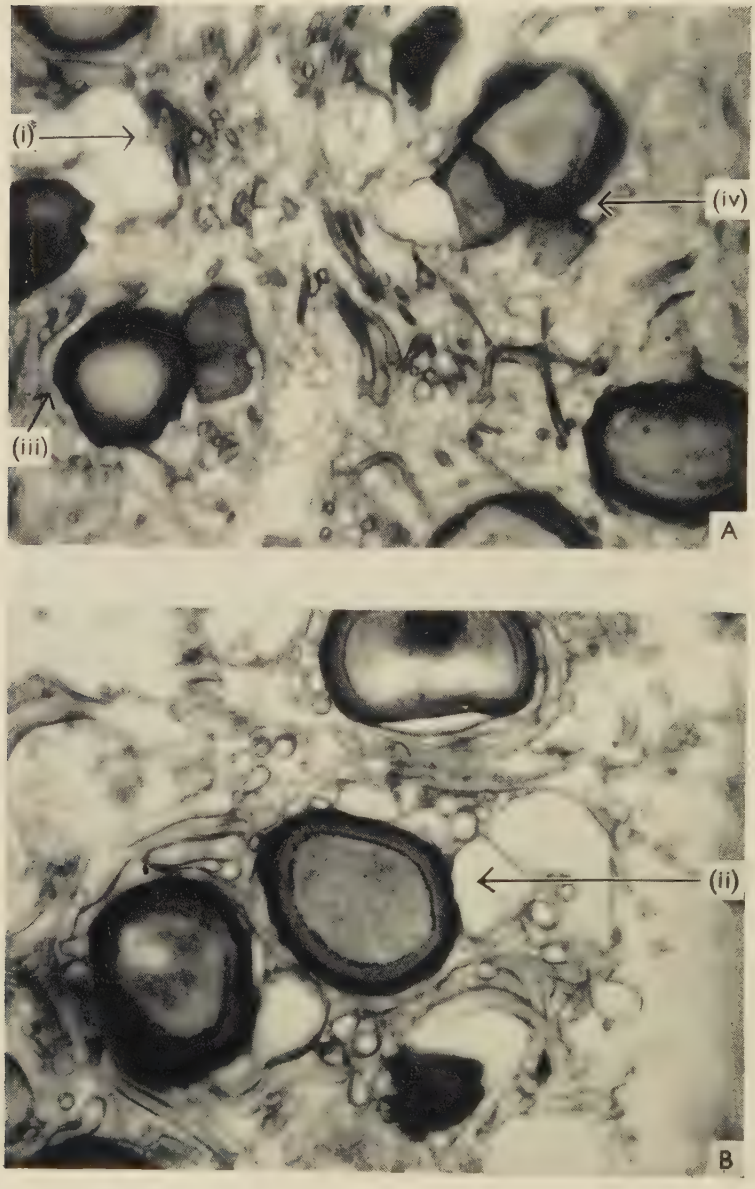

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EXPLANATION OF PLATE 6

Endogone microcarpa, sections through zygosporic area of a fruit-body which contained both zygospores and chlamydospores. Empty paired gametangia and suspensor cells are seen in A (i); the section has not gone through the zygospore. A single empty gametangium and suspensor with attached thick-walled zygospore is seen in B (ii); the other gametangium is not in the plane of the section. Zygospores in which the endospore lines both spore and gametangia are seen in A (iii) and (iv).

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Addendum

In a recent paper (Petitberghien, P. (1956), 'Les champignons hypogés de la région de Dijon', *Bull. sci. Bourgogne*, **16**, 115–155), chlamydospores of *E. microcarpa* apparently supported by two subtending hyphae are figured. On morphological grounds these are considered to be chlamydospores rather than zygospores, an interpretation which is vindicated by the discovery during the present study of undoubted zygospores of the fungus. The spores with two supporting hyphae, figured by Petitberghien and others, are best interpreted as chlamydospores borne on short lateral hyphal branches or in an intercalary position.

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STUDIES OF BRITISH SPECIES OF *ENDOGONE*

II. FUNGAL PARASITES

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(With 1 Text-figure)

Chlamydospores of four species of *Endogone* were frequently invaded by fungal hyphae. The yellow-spored type of *E. macrocarpa* was invariably parasitized and similar parasites were seen in other types of this species, in some, but not all, fruit-bodies of *E. microcarpa*, in *E. fuegiana* and in a single fruit-body attributed to the *E. fasciculata–E. vesiculifera* group. The hyphae of the gleba were also occasionally invaded. A slow-growing, non-sporing, septate mycelium was isolated from infected spores. That from spores of *E. microcarpa* differed in rate of growth from those from other host species. A comparison was made with parasites of *Endogone* described by earlier writers.

Parasitism was closely correlated with the presence of fine radial canals in the chlamydospore walls. Occasionally conical projections of the wall developed opposite the radial canals which sometimes penetrated through them. Penetration by the parasite took place through these canals. The significance of the canals and inward projections of the wall is discussed.

Introduction

During a study of British species of *Endogone* (Godfrey, 1956) chlamydospores of *E. microcarpa*, *E. macrocarpa* and *E. fuegiana* have frequently been found to contain hyphae of parasitic fungi. A single fruit-body attributed to the *E. fasciculata–E. vesiculifera* group was similarly parasitized and one fruit-body of the zygosporic species, *E. lactiflua* showed invading hyphae penetrating the gleba.

Thaxter (1922) recorded parasitic attack in *E. vesiculifera*, *E. lactiflua*, *E. fuegiana* and other species and illustrated chlamydospores of *E. fuegiana* almost filled with a mass of hyphae.

Malençon (1947) described two fruit-bodies of *E. microcarpa* which were parasitized by a species of *Cephalosporium*. The chlamydospores (interpreted as azygospores by Malençon) and the ground tissue of the gleba were invaded by parasitic hyphae. Brownish sclerotia were formed in some of the spores, and oidia were also observed. Small chlamydospores were formed by the *Cephalosporium* at the periphery of the fruit-body and occasionally within the *Endogone* spores. Malençon described fine radial canals in the chlamydospore wall and conical projections from the inner surface of the endospore and suggested that the parasite gains entry to the spore by way of these canals. He compared the projections with similar structures observed by Foëx & Rosella (1930) in wheat straw invaded by *Ophiobolus graminis*. Malençon was unable to reach a definite conclusion as to whether the canals were a morphological character of certain *Endogone* fruit-bodies or whether they arose as a result of an outside influence.

Similar radial canals in the spore wall of *E. macrocarpa* had been observed by Bucholtz (1912), but he had thought that they were closed at both ends. Thaxter (1922) referred to them in a collection of *E. macrocarpa* fruit-bodies and considered that they were associated with masses of oily material adhering to the inner surface of the spore wall.

More recently, Mosse (1954) described fine hyphae within the chlamydospores of a species of *Endogone* found in association with mycorrhizal strawberry roots (see Godfrey, 1956). Mosse states that the apparent germination of some of these spores by a number of fine germ tubes (Mosse, 1954, fig. 35) was interpreted by Dr R. W. G. Dennis of the Herbarium, Royal Botanic Gardens, Kew, as the emergence of hyphae of the parasite, which may have been an Actinomycete. Mosse finally concluded from a consideration of the cultural characters of isolates of such hyphae that they were indeed those of an actinomycetous parasite which she considered to be a species of *Micromonospora*. Small lemon-shaped spores were also observed by Mosse and compared with similar ones described by Peyronel (1923). It would seem unlikely that these are produced by the Actinomycete. Mosse concluded that the actinomycetous parasite had probably entered through the fine canals which were visible running through the centre of internal projections of the spore wall.

Before seeing the account of Mosse's work the writer had made independent observations of parasitized spores and had associated fine radial canals seen in the spore wall or running through the internal projections of the endospore with the entry of the parasite. In view of the contradictory nature of previous accounts of parasitism in *Endogone* all collections made were examined for signs of parasitic invasion.

Morphology of parasitized fruit-bodies

Endogone microcarpa

Parasitized fruit-bodies have been collected during the past two years from Somerset, Kent and Northumberland. The nature of the parasite was similar in material from all areas. In the Bristol area, about ninety of the fruit-bodies collected were parasitized. Occasional uninfected specimens have been recorded from the same sites as the infected ones.

In a severely parasitized fruit-body all the spores, including the young ones, are likely to contain parasitic hyphae (Fig. 1 A–D), and the parasite may be present within the matrical hyphae of the fruit-body. With a less severe infection, not all the spores are invaded.

The frequency of radial canals in the spore wall varies, but often there are 8–20 per spore. Projections may be associated with some of the canals (Fig. 1 C), but in many fruit-bodies they are lacking. Projections or canals alone may also be observed in the larger hyphae of the ground tissue, but they are not frequent.

In its most characteristic form the parasite is not readily observed within the spores. The hyphae are very thin-walled, septate, and they swell up to become about 6μ diam. The spores containing these swollen hyphae have the appearance of being filled with a number of large honeycomb-like cells.

In young specimens the spores and hyphae of *E. microcarpa* contain oil-droplets and granules, and the thin-walled hyphae of the parasite are hard to discern. In very old fruit-bodies the spores and parasitic hyphae are empty of protoplasmic contents, and the parasite shows up clearly. Narrower parasitic hyphae (2–3μ diam.) may be seen in some of the

Fig. 1. A–D, parasitized spores of *E. microcarpa*; E, part of young spore of *E. macrocarpa*, yellow spored type, showing invading hyphae and mantle of parasitic hyphae surrounding the spore. F, parasitized spore of *E. fuegiana*. G, section of spore wall in *E. macrocarpa*, yellow spored type, showing radial canals, two of which pass through short projections on the inside of the endospore. Note internal projections (*p*) of spore wall in C, where radial canal does not reach tip of projection; and in F, where penetration has taken place through the central canal.

spores. These presumably represent a condition in which the hyphae have not swollen up in the typical fashion. There is no reason to believe that they belong to a different species of parasite.

Since the chlamydospore is usually in open connexion with its stalk, the parasitic hyphae are free to pass into the *Endogone* hyphae and have occasionally been observed within the larger ones.

The parasitic hyphae may grow freely among the *Endogone* matrical hyphae, when they are easily distinguished by their thin walls. In one or two specimens they have been observed forming a sheath of thin-walled, swollen elements about individual spores. This sheath effect is rare in its occurrence.

Extramatrical chlamydospores of Endogone microcarpa. The finding of wefts of hyphae and extramatrical chlamydospores in association with *E. microcarpa* fruit-bodies is described by Godfrey (1957). These fruit-bodies often contained parasitized spores, but the extramatrical spores showed no signs of being infected, and radial canals were not present in their walls. The loose hyphae were seldom attacked.

Definite branched white strands, about 70μ diam., leading from the fruit-bodies, were often present among the loose *Endogone* hyphae. The strands were composed of closely packed hyphae which resembled those of the parasite. The production of similar strands in culture is described on p. 141. One strand was usually associated with a single fruit-body and could be readily detached from it. New fruit-bodies are laid down in the loose mycelium and the spread of the parasite from one fruit-body to the next can presumably take place by means of these infection strands. In one instance, an extremely young fruit-body forming in the loose mycelium round a mature parasitized one was found to be uninfected. Usually, however, the young fruit-bodies adjacent to mature ones were parasitized.

Endogone macrocarpa

The variation within *E. macrocarpa* has been described by Godfrey (1956, 1957). Fruit-bodies of the yellow-spored type have invariably been found in a parasitized condition, but amongst the remaining types only two cases of parasitism have been recorded.

A most noticeable feature of the spore wall of the yellow-spored type of *E. macrocarpa* is the presence of very numerous radial canals (Fig. 1 E, G). There may be 100 or more in a single spore. Projections from the inner surface of the endospore may be very abundant, although they are not present in all fruit-bodies. Sometimes the projections are massive and traversed by two or three canals, sometimes they are slender and crowded together. Canals and projections may be frequent in the matrical hyphae, particularly in those bearing chlamydospores.

The spores are filled with a mass of interwoven hyphae, sometimes so densely compacted that at low magnification the appearance is that of normal spore contents. Within the spore, the hyphae are about 3–5μ diam., septate, thin-walled, with greyish protoplasmic contents. They are sometimes swollen but usually retain the normal diameter. The parasite may be seen within the matrical hyphae of the fruit-body, even when the diameter of these is such as to admit only one parasitic hypha. In the older specimens devoid of protoplasmic contents, other types of hyphae may be present within the *Endogone* hyphae. A mycelium with clamp connexions was noticed in one instance. These hyphae are probably stray invaders which have penetrated the fruit-body after it has become moribund.

The parasite is usually conspicuous amongst the ground tissue of the fruit-body. It tends to form a definite layer round the individual spores, particularly the younger ones. This 'sheath' may be a very prominent feature in some fruit-bodies, but in others it is scarcely noticeable. The hyphal elements of the sheath are thin-walled and swollen, but discrete hyphae about 3–5μ diam. may also be observed. The sheath effect is similar to that occasionally seen in *E. microcarpa*, but it is more extensively developed.

A single fruit-body of the golden-spored type was recorded in which a few of the spores were parasitized. The older spores contained parasitic hyphae, while some of the young thin-walled spores contained a mass of oidial cells. No growth took place from the oidia when they were transferred to plain agar, but when a whole infected chlamydospore containing these was placed on agar, a few hyphae grew out from it. There seems to be no doubt that the oidial cells belonged to the parasite.

An example of parasitism was recorded in a fruit-body of intermediate type which closely resembled the golden-spored type, but differed from it in the colour of the spores. A few radial canals and small projections were present in the spore wall. The parasitic hyphae in this specimen were not of the type previously described, being about 1·5μ or less in diameter. The terminal branches of the hyphae were often very fine and scarcely distinguishable. The parasite was present in some of the ground hyphae of the fruit body, as well as in the spores. It was also visible as a faint sheath, about 10μ wide, surrounding the individual spores. Attempts to isolate this parasite on agar were unsuccessful, probably because the specimen was old and the hyphae dead.

Endogone fuegiana

Fruit-bodies collected from various parts of Goblin Coombe, Somerset, have all been parasitized. Occasional spores have shown no traces of the parasite, but they have been very rare. Both young and old spores were infected. A single, very young specimen from Wraxall, Somerset, was not parasitized.

The infected spores are filled with a woven mass of hyphae, 3–6μ diam. similar to that in the yellow-spored type of *E. macrocarpa* (Fig. 1 F). Canals and projections are less numerous than in the latter species and resemble those of *E. microcarpa* in their frequency.

Traces of the parasite are sometimes visible within the hypha bearing a group of chlamydospores, but the parasite tends to be confined to the spores even when a septum is not present to separate the spore from the parent hypha.

The parasitic hyphae are often densely packed between the spore groups in the ground tissue and it is sometimes difficult to distinguish between the hyphae of *Endogone* and those of the parasite. The spores are not readily freed from the surrounding hyphae when such a parasitized fruit-body is teased out.

Fruit-body of Endogone fasciculata–E. vesiculifera *group*

The single fruit-body described by Godfrey (1957) was parasitized. The spores were old and contained only remnants of dead hyphae. Simple canals were present in the spore walls, but no projections were observed.

Isolation of parasites from infected spores

Methods

Infected chlamydospores were placed on plates of water agar (1·5 % agar) and incubated at 20° C. The parasitic hyphae grew out readily within 2 or 3 days. They emerged through the radial canals in the chlamydospore walls or through the broken end of the parent hypha. Small portions of the mycelium were transferred to a variety of nutrient media but no spores were produced. Malençon (1947) induced sporulation in a species of *Cephalosporium* isolated from fruit-bodies of *Endogone microcarpa* by growing the fungus in hanging drops of distilled water. Similar treatment did not cause spore production by any of the parasites isolated by the present writer.

Cultural characters of isolates from Endogone microcarpa

Water agar. Colony thin, white, aerial mycelium scanty, 8 mm. diam. at eighteen days, hyphae thin-walled, greyish hyaline, occasionally septate, 2–3μ occasionally 4μ wide, branched at an acute angle or at right angles, branches ending bluntly, sometimes slightly constricted at base.

Malt agar (1 %). Compact, white colony, flat at periphery, somewhat wrinkled in centre with fluffy aerial mycelium, 2–3 mm. diam. at eighteen days, with branched white strands (*c.* 50μ thick), composed of aggregated hyphae, radiating from centre of colony. Growth slightly better on 3 % malt agar.

Oatmeal agar. Thin white colony, 8 mm. diam. at eighteen days, some aerial mycelium, edge of main colony irregular, hyphal strands radiating outwards as on malt agar.

Potato-extract agar. Growth similar to that on oatmeal agar. Colonies on all these media odourless, medium unstained.

Cultural characters of isolates from Endogone macrocarpa *and* E. fuegiana

Water agar. Colony delicate, feathery appearance, growth rate variable, approximately 12 mm. diam. at 18 days, hyphae mainly submerged but a little white aerial mycelium present. Hyphae thin-walled, greyish hyaline, occasionally septate, 1·5–4·0μ wide, branched at an acute angle or at right angles, tendency to localized patches of more densely branched hyphae near centre of colony.

Malt agar (1 %). Fairly compact colony, greyish white, 12–16 mm. diam. at 18 days, hyphae mainly submerged, but some aerial mycelium at centre, often irregular patches, edge of colony irregular, branched white hyphal strands (50μ or less thick) radiating outwards at surface of colony. Growth on 3 % malt similar.

Oatmeal agar. Colony thin, dingy white, 10 mm. diam. at 18 days, hyphae mainly submerged, hyphal strands as on malt agar.

Potato-extract agar. Similar but growth rather slower. Colonies on all these media odourless, media unstained.

Comparison of isolates with other recorded parasites of Endogone

The isolates from *E. microcarpa* differ from those from *E. macrocarpa* and *E. fuegiana* mainly in slower growth and lack of colour in culture. Both types of isolates are obviously fairly closely related. Owing to the absence of spores it is not possible to identify them but the occasional septa and the development of hyphal strands suggests that they are either Ascomycetes or Basidiomycetes. The absence of clamp connexions does not necessarily exclude them from the latter group.

It is not possible to judge from the single figure given by Thaxter (1922) whether the parasite found by him is identical with those described in this paper. Nothing resembling the lemon-shaped spores observed by Peyronel (1923) in vesicles of a root endophyte, believed by him to be an *Endogone*, has been observed. The sclerotia and small chlamydospores produced by the species of *Cephalosporium* from fruit-bodies of *Endogone microcarpa* (Malençon, 1947) were not seen in any of the material but oidia were occasionally seen. There is no evidence that the parasites described in this paper are a species of *Cephalosporium*. The hyphae observed by Mosse (1954) growing out from chlamydospores of her unidentified species of *Endogone* were much finer and were attributed by her to an Actinomycete. She also observed spores similar to those described by Peyronel. The parasites isolated in the present study bore no resemblance to an Actinomycete but very fine parasitic hyphae were observed in one fruit-body of *E. macrocarpa* (p. 139). These were not isolated. It is likely that the spores of *Endogone* are liable to attack by more than one parasite.

Significance of radial canals and ingrowths of endospore

Parasitism in the chlamydosporic species of *Endogone* is closely correlated with the presence of radial canals in the spore wall. The spores are invaded only when canals are present and entry of the parasite takes place through them. Conversely, almost all spores with canals in the walls contain parasitic hyphae but occasionally spores with such canals may be entirely empty of contents. These may represent the last stage in attack when destruction of the spore contents has been followed by autolysis of the parasitic hyphae. Such spores are found only in fruit-bodies containing typically parasitized ones.

The canals might be a definite structural feature which happens to render the spores more liable to infection or they may be formed in response to the presence of the parasite or by direct action of the latter.

The fact that canals are a constant feature in the yellow-spored *E. macrocarpa* might suggest that they are a normal structural character of the wall of this type, were it not for the presence of similar canals in some fruit-bodies of the golden-spored and other types. Thaxter (1922) thought that the

radial canals in his material of *E. macrocarpa* were associated with the presence of oily material in the spores and makes no mention of the spores being parasitized. Too much importance should not be attached to such negative evidence, since Thaxter was not primarily interested in the parasite. Moreover, it has been shown above (p. 138) that the parasitic hyphae are often difficult to distinguish and that large oil droplets are a prominent feature of parasitized spores.

There is more evidence to support the alternative view that the canals are formed as a result of parasitic attack. First, fruit-bodies containing spores with canals are by no means invariable in *E. microcarpa*. There are no grounds for suggesting that the fruit-bodies with radial canals constitute a different variety from those without, for intermediate-type fruit-bodies exist in which only a small percentage of the spores exhibit canals. The canals cannot therefore be regarded as a constant structural feature in *E. microcarpa*.

Secondly, the nature of the canals points to their being formed as a result of an outside influence. Attention has already been drawn to the fact that the canals begin from the outer surface of the spore and may not penetrate completely to the inner one. They may best be interpreted as the result of successful or unsuccessful attempts by the parasite to penetrate the chlamydospore wall. It may be postulated that the projections of the wall, which often accompany the radial canals, represent a localized reaction of the spore wall against penetration by the parasite. Such a reaction of the host wall as a result of attempted penetration by a parasitic fungus is frequently shown by higher plants, e.g. the 'lignitubers' seen in wheat roots and haulms invaded by *Ophiobolus graminis* (Fellows, 1928; Foëx & Rosella, 1930), in roots of *Myrica gale* invaded by the nodule organism (Hawker & Fraymouth, 1950) and in numerous plants attacked by downy mildews (Fraymouth, 1956).

It is probable that the projections occur when a young spore is attacked while the thickening of at least part of the endospore is still proceeding. As the penetrating hypha passes through the developing wall, material is laid down opposite the advancing canal and an inward projection of the endospore is thus formed. The length of the projection may perhaps be correlated with the age of the spore when penetration began. When a mature wall is penetrated no such response is possible and a radial canal without any corresponding projection of the host wall results.

With the exception of the radial canals and projections, there is no evidence that parasitism brings about pronounced morphological changes in the fruit-bodies. In *E. microcarpa*, for example, the spore colour, thickness of the wall and size of spores is much the same in parasitized and unparasitized fruit-bodies. There is nothing to suggest that parasitism might account for the distinction between the various types of *E. macrocarpa*.

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Addendum

Fungal parasites in chlamydospores of *E. microcarpa*, associated with internal projections of the wall and fine penetration canals, have recently been described from France (Petitberghien, P. (1956), 'Les champignons hypogés de la région de Dijon', *Bull. sci. Bourgogne*, **16**, 115–155). The figures suggest that the parasite is not identical with that described in the present paper. Spores of *E. macrocarpa* contained no fungal parasites.

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SOME EFFECTS OF PEA ROOT EXUDATES ON PHYSIOLOGIC RACES OF *FUSARIUM OXYSPORUM* FR. F. *PISI* (LINF.) SNYDER & HANSEN

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(With 4 Text-figures)

Exudates from the roots of the pea cultivars, Onward, Alaska and Delwiche Commando, which differentiate between three physiologic races of *Fusarium oxysporum* f. *pisi*, affected spore germination in the three races differentially, depressing the germination of races they resisted more than of those to which they were susceptible. Exudates from young seedlings depressed germination more than did those from roots of older plants, and the activity of exudates increased temporarily when side roots were first formed.

When concentrated root exudates were contained in porcelain cylinders on agar sown with spores, zones of differential growth formed around the cylinders; when the exudate was from a cultivar resistant to the race whose spores were plated, the zone was one of growth inhibition, and when from a susceptible cultivar, it was one of growth stimulation. Notwithstanding this effect on spore germination, exudates from the different cultivars had no differential effect on the rate at which germ tubes or mycelium of the individual races grew.

Sections through roots of cultivars inoculated with a race they resist showed that the mycelium invaded only the outer cortex.

Plants susceptible to *F. oxysporum* wilt less when simultaneously infected with *F. solani*; extracts of the bases of pea plants infected with *F. solani* inhibited the germination of spores of *F. oxysporum*, whereas extracts from normal stem bases did not.

Introduction

In common with most pathogenic fungi, *Fusarium oxysporum* Fr. f. *pisi* (Linf.) Snyder & Hansen (cause of pea wilt) occurs as physiologic races, distinguishable by their abilities to affect different pea cultivars, and three of which are differentiated on pea cultivars Onward, Alaska and Delwiche Commando (Schreuder, 1951; Buxton, 1955). A full consideration of the mechanisms by which pea cultivars resist particular races should include not only conditions inside plants but also those on or near the root surface (rhizosphere region), where the fungus must grow successfully before it can invade roots. Whether or not the pathogenic differences between physiologic races of *F. oxysporum* f. *pisi* are determined before or after the roots are invaded is unknown, but the present paper records results showing that root exudates from different pea cultivars can affect the physiologic races in different ways.

Materials and methods

The three physiologic races of *F. oxysporum* f. *pisi* were derived from the following sources: race 1, isolated from wilted peas cv. Onward, from Essex, England; race 2, from wilted peas (cv. not known), from Wisconsin,

U.S.A.; race 3, from wilted peas var. Meteor, from Essex, England. The three pea cultivars that differentiate these races are Onward, susceptible to all three; Alaska, resistant to race 1 but susceptible to races 2 and 3; Delwiche Commando, resistant to races 1 and 2, but susceptible to race 3. Onward seed was obtained from Messrs Sutton and Sons Ltd., Reading, England; Alaska and Delwiche Commando seed from the Ferry Morse Seed Co., U.S.A.

Three methods were used to obtain exudates from pea roots growing under sterile conditions. In one, peas were placed in sterile glass-distilled water (one pea per 10 ml. of water) in Petri dishes and left at room temperature (15–18° C.) in daylight. In another, 200 g. autoclaved washed quartz sand and 100 ml. of sterile glass-distilled water were put in 1 l. conical flasks. Three peas were sown in the sand and the flasks were plugged with cotton-wool and kept in daylight at room temperature. In the third method, a modified soil perfusion apparatus, similar to that described by Audus (1946) and containing 10 cm. columns of autoclaved sand, was used. Three peas of one differential cultivar were placed separately in each of six sand columns through which 100 ml. sterile glass-distilled water was circulated. After various periods of growth, all the water was removed from the apparatus used in each of the three methods, which were run concurrently. The combined water from each method was then separately concentrated under a vacuum in sterile 1 l. conical flasks at 40° C. to one-fifth of its original volume (i.e. concentration 5 V, where V = concentration of the original). This was done because preliminary tests showed that the biologically active properties of the exudates were inactivated by boiling and were not evident at low concentrations. Four methods were used to test how the exudates from the three cultivars affected the different physiologic races:

(1) Spore germination in the exudates was counted.

(2) Mycelial growth rate was measured on agar media containing exudate.

(3) Mycelium grown in flasks containing exudate was dried and weighed.

(4) The effect of exudates contained in porcelain cylinders on agar containing spores was observed.

Experimental results

Effects on spore germination

Tests were made on spores from 12-day-old cultures of each physiologic race suspended in sterile glass-distilled water. After adjusting to 2×10^6 per ml. by haemocytometer count, 0·5 ml. spore suspension was added to 0·5 ml. exudate (concentration 5 V) in test-tubes. Control tubes contained spores in sterile water, and in sterile water which had circulated through sterile sand. Germinated spores were counted and germ-tube lengths were measured after 5 days incubation at 25° C. At intervals of 5 days from sowing the peas, all the water was replaced and tested to find whether or not any change in the root exudate could be correlated with different stages of the plants' growth.

In exudates from young roots of var. Onward, spores of all three races germinated well, but exudates from older roots depressed germination of all three. Exudates from var. Alaska differentiate the races clearly, for race 1 germinated very poorly in it; Delwiche Commando root exudate

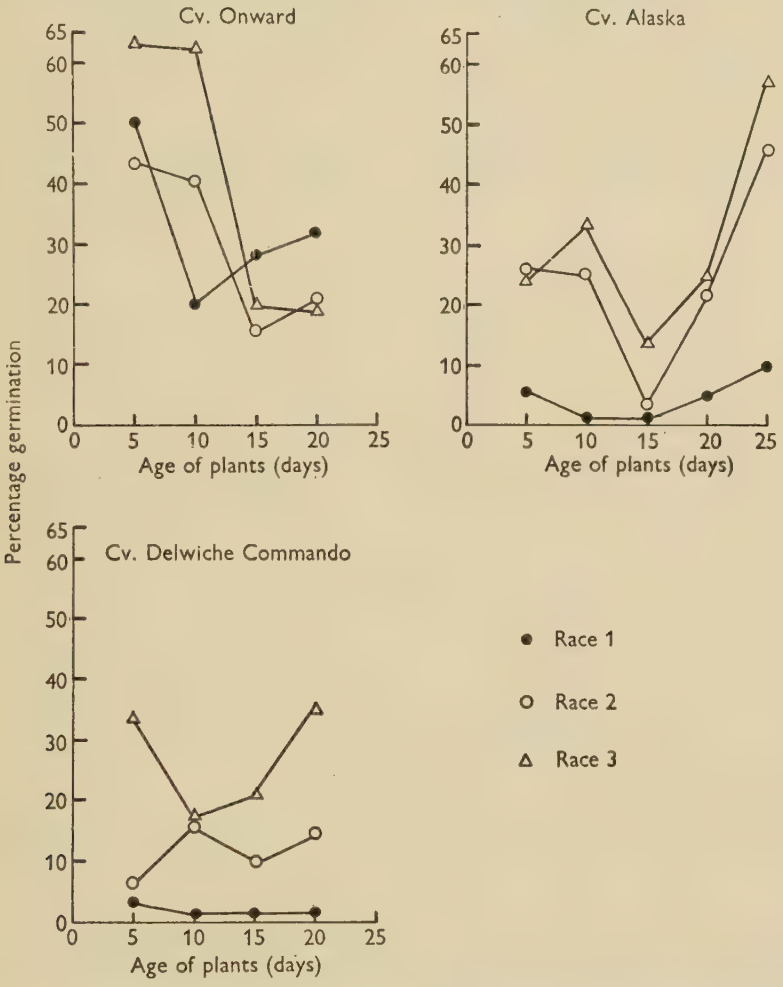

Fig. 1. Germination of three physiologic races of *F. oxysporum* f. *pisi* in root exudates of three differential pea cultivars.

almost prevented spores of race 1 from germinating and severely depressed germination of race 2. Hence, effects on germination were correlated with the resistance of the host to infection by a race. Inhibitory effects on germination were greatest when exudates were from plants about 15 days old and, from Alaska, also when 5 days old. After 10–12 days from planting, side-roots appeared along the whole length of the main roots and this may be responsible for the increased exudation at that time of substances that

affect the spores. Although primary roots and secondary roots were measured and their surface areas computed at each stage of the experiments, no correlation was apparent between the measurements and the effects of exudates on the spores.

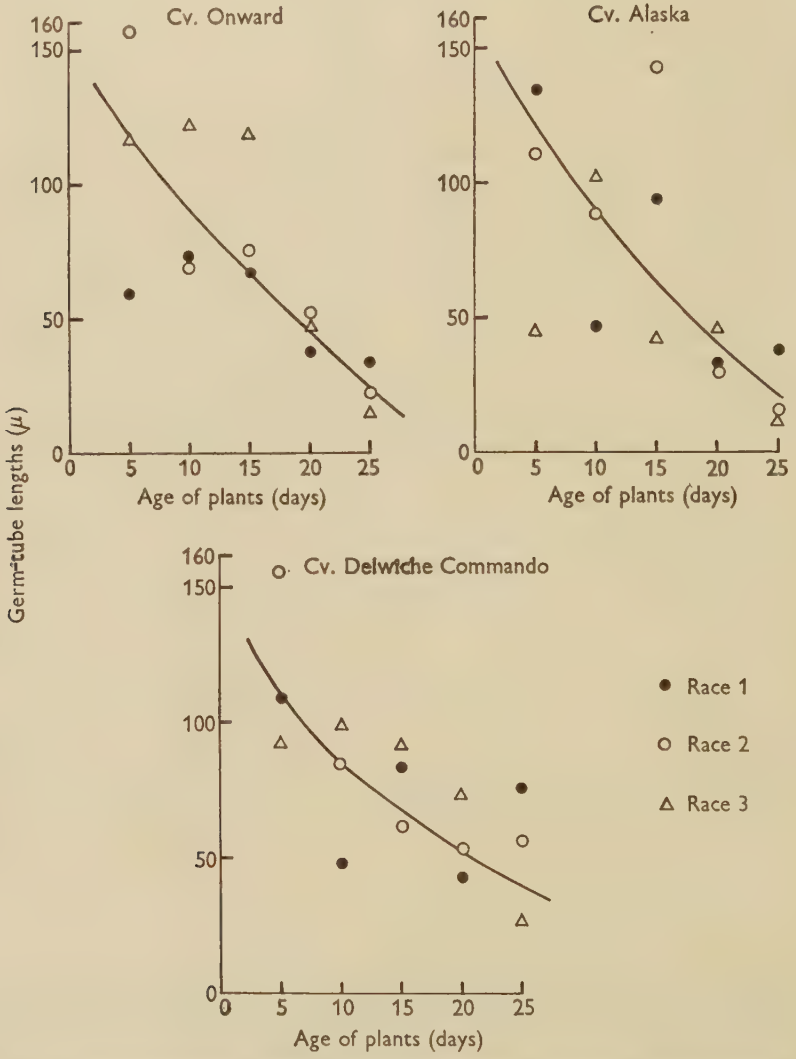

Fig. 2. Germ-tube lengths of three physiologic races of *F. oxysporum* f. *pisi* growing in root exudates of three differential pea cultivars.

The lengths of germ tubes were measured in all the tests to see whether their growth was also differentially depressed by the exudates.

Although germ tubes of all three races grew well in exudates from young plants, they grew less well in exudates from older plants. This is probably

because the concentration of substances which specifically suppress the growth of germ tubes is higher in exudates from older plants, whereas the concentration of other substances, which adversely affect spore germination, decreased when the plants were 25 days old (Fig. 1). No one exudate specifically depressed the germ-tube lengths of any particular race of the fungus; the main differential effect of the exudates thus appears to be on spore germination.

Effects on growth on agar media

Dishes separately containing 5 ml. of the three exudates in 15 ml. of Czapek-Dox agar (exudates introduced when the agar was at 45° C.) were inoculated with 3 mm. disks of young mycelium from 5-day-old agar cultures of races 1, 2 and 3.

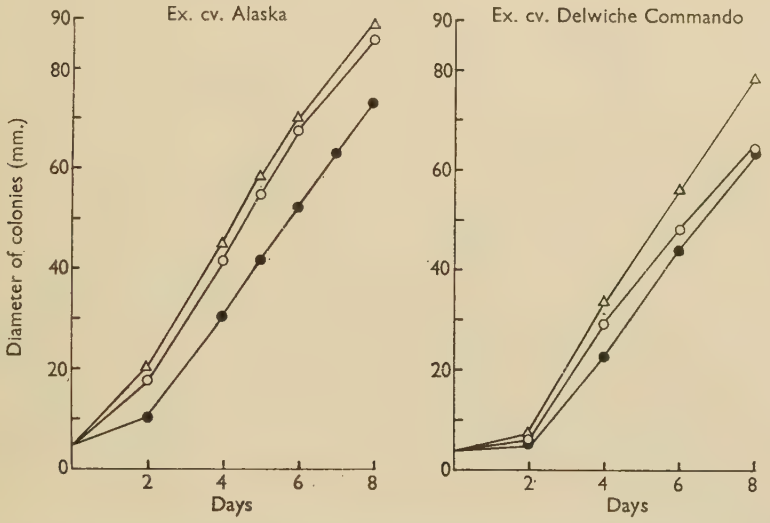

Fig. 3. Growth rates of three physiologic races of *F. oxysporum* f. *pisi* on agar to which root exudate of pea cv. Alaska or Delwiche Commando have been added. ●, race 1; O, race 2; △, race 3.

On agar containing Alaska root exudate, races 2 and 3 grow better than race 1, which was delayed for 2 days. All three races have an initial lag on agar containing exudate from Delwiche Commando, but race 3 ultimately grows better than races 1 and 2. All three races may grow more slowly on medium containing exudate from Delwiche Commando than on that from Alaska because Delwiche Commando produces more inhibiting substances.

In another experiment testing the effects of exudates on mycelial growth rates, 100 ml. flasks containing 25 ml. exudate (5 *V*) were inoculated with aliquots of spores of the three races. Dried mycelial mats, obtained after 20 days growth at 25° C., showed no significant differences in weight. Presumably spore germination was initially suppressed in some flasks

(cf. Fig. 1) and any viable spores remaining would ultimately have produced an amount of mycelium equal to those produced by spores of races which had been affected by exudate.

The effects of exudates on spores in agar were tested by putting 0·3 ml. concentrated (10 *V*) exudates into porcelain cylinders placed in dishes of Czapek-Dox agar which separately contained spores of the three races. Inhibition zones or zones of enhanced growth appeared round the cylinders and were recorded after 48 hr.

Table 1. *Inhibition zones in three races of* Fusarium oxysporum *f.* pisi *caused by concentrated root exudates from pea*

(Diameter of zones (mm.).)

	Physiologic races		
Pea cultivar	1	2	3
Onward	0	0	0
Alaska	20·1	Increased growth	0
Delwiche Commando	14·3	16·6	0

The effects are again correlated with the pathogenic capabilities of the three physiologic races towards the three host differential cultivars. Alaska exudate strongly inhibited race 1 and increased the growth of race 2. The inhibition zones contained spores which had not germinated, and later the mycelium on the edge of these zones grew towards the porcelain cylinders. This phenomenon implies that the exudate is not fungicidal, but deters germination and, to a less extent, mycelial growth. This technique provides a second method of differentiating between physiologic races of *F. oxysporum* f. *pisi in vitro*; the only previous method came from the observation that different physiologic races were inhibited to different extents by the growth products of certain actinomycetes (Buxton & Richards, 1955).

To find whether the effects of pea root exudates are specific to *F. oxysporum*, four other soil-borne fungi, all isolated from potato, were tested in agar by the porcelain cylinder method. The effects of potato root exudate, which promotes the hatching of cysts of potato eelworm, *Heterodera rostochiensis* Wollenw., were also tested. Pea root exudates (from cv. Alaska) had no effect on *Colletotrichum atramentarium* (Berk. & Br.) Taubenh., *Rhizoctonia solani* Kühn and *Oospora pustulans* Owen & Wakef., but slightly inhibited *Phytophthora infestans* (Mont.) de Bary. It did not promote hatching of eelworm cysts. Potato root exudate promoted growth of *P. infestans* and inhibited race 1 of *Fusarium oxysporum*, but much less than did Alaska exudate. It had no effect on the other three fungi, but slightly inhibited races 2 and 3 of the *F. oxysporum*.

Filter-paper chromatograms showed that the exudates contained small amounts of amino-acids and sugars, but neither these nor spectrophotometer measurements showed any differences between exudates from roots of the three pea cultivars.

Rate of root penetration by physiologic races

F. In addition to studying the effects of root exudates on the races of *f. oxysporum*, the rates at which they penetrate roots of the three host cultivars were examined. Inoculated plants, grown in pots containing

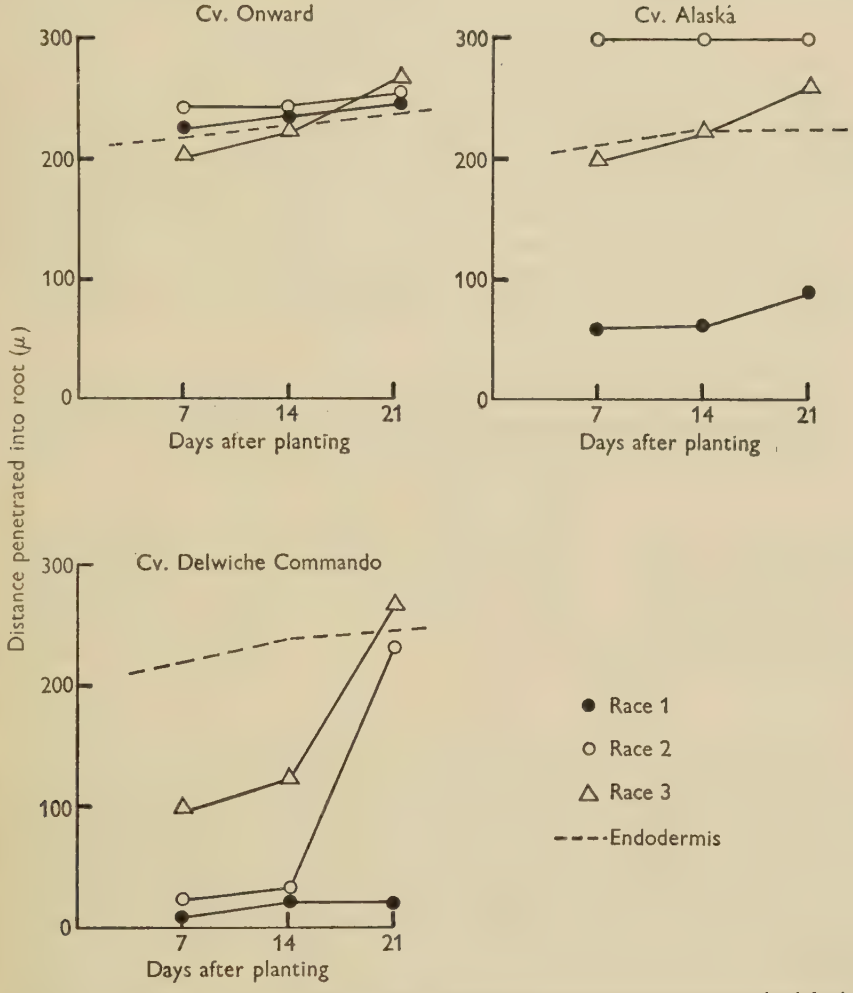

Fig. 4. Penetration rates into roots of three differential pea varieties by three physiologic races of *F. oxysporum* f. *pisi*.

unsterilized John Innes potting compost, were sampled after 7, 14 and 21 days from the time of inoculation. Randomly selected parts of roots, of diameter 1 mm. or less, were sectioned (freezing microtome) and the distances to which fungus mycelium had penetrated were measured.

Onward plants were soon penetrated and the mycelium of each of the three races quickly established itself in the inner cortex and vascular tract.

Race 3 penetrated the vascular tract of all three varieties, but did so more slowly. The results, given in Fig. 4, show effects of the host on fungus invasion which parallel those with exudates on spore germination (Fig. 1 and Table 1). Plants susceptible to races 1 and 2 began to wilt 12 days after inoculation, but plants infected with race 3 did not wilt until after 18 days.

Effect of previous inoculation with Fusarium solani

When peas inoculated with *F. oxysporum* f. *pisi* race 1 are inoculated simultaneously with *F. solani* f. *pisi* (Jones) Snyder & Hansen (cause of foot rot of peas), or with non-pathogenic *F. solani*, plants are much less affected than when inoculated with *F. oxysporum* f. *pisi* alone (Buxton, 1955). To test whether *F. solani* produces any substances *in situ* that inhibit the growth of *F. oxysporum*, plants of the variety Onward were inoculated separately with *F. solani* f. *pisi* and with non-pathogenic *F. solani*. Sterile water extracts were made of the stem bases of inoculated and uninoculated plants and divided into two lots, one filtered to remove possible bacterial contaminants, the other autoclaved at 15 lb. pressure for 15 min.

Table 2. *Effects of extracts from stem bases of peas var. Onward, inoculated with pathogenic and non-pathogenic* Fusarium solani, *on the germination of spores of* F. oxysporum *f.* pisi *race* 1

Inoculum used	Patho-genic *F. solani*	Patho-genic *F. solani*	Non-patho-genic *F. solani*	Non-patho-genic *F. solani*	Nil	Nil
Post-extraction treatment	Filtered	Auto-claved	Filtered	Auto-claved	Filtered	Auto-claved
Percentage germination after 4 days	0	8·7	1·0	13·8	23·8	28·6
Percentage germination after 8 days	6·3	25·7	5·0	25·9	43·1	36·6

Table 2 shows that the spore germination of *F. oxysporum* was depressed in extracts from plants inoculated with the two isolates of *F. solani* but not in extracts from uninoculated plants. Autoclaving destroyed the toxicity of substances extracted from inoculated stem bases, whether they showed foot-rot lesions or whether they were inoculated with non-pathogenic *F. solani*. When concentrated extracts were added to porcelain cylinders on Czapek-Dox agar containing spores of *F. oxysporum* race 1, inhibition zones formed (Table 3).

Table 3. *Inhibition zones in* Fusarium oxysporum *f.* pisi *race* 1 *caused by extracts of lesions due to* F. solani *f.* pisi *on pea*

(Diameter of zones (mm.).)

Lesion caused by *F. solani* f. *pisi*		Stem inoculated with non-pathogenic *F. solani*	
Filtered	Autoclaved	Filtered	Autoclaved
13·0	0	19·0	0

Culture filtrates of *F. solani*, pathogenic and non-pathogenic (grown in liquid Czapek-Dox medium) had no effect on spore germination of *F. oxysporum*; nor was there any interaction between the two species when grown together on agar media. The effect on *F. oxysporum* spores was evident only when *F. solani* was grown on peas, and the depression could obviously play a part in decreasing the wilt symptoms when the two species occur together in infected plants.

Discussion

Whether the effects of root exudates on the germination of *Fusarium oxysporum* spores demonstrated here plays any part in determining the resistance of pea varieties to different races of the fungus is uncertain. If it does, then it seems that the resistance depends in part on something that happens before the plant becomes infected. Obviously, if resting spores or mycelium in the rhizosphere do not germinate, they will not penetrate the root. The exudates, which presumably would occur in the rhizosphere in higher concentrations than those used in these experiments, could act by decreasing the potential inoculum. Many other factors, and particularly the metabolic activities of other rhizosphere micro-organisms, could be expected to interfere with the activity of the exudates.

Because exudates differentially affect the growth of individual physiologic races, this does not necessarily imply that resistance is wholly localized on the root surface. It is more likely that resistance is not specifically related to any particular region in the host plant. In peas, races of *F. oxysporum* non-pathogenic towards particular host varieties are deterred at all stages of their growth from the root surface into the cortex. Heinze & Andrus (1945), working with tomato, also found that roots of resistant varieties were not deeply penetrated by *F. oxysporum* f. *lycopersici* (cause of tomato wilt). Snyder, Baker & Hansen (1946) and Scheffer & Walker (1954), however, demonstrated that some resistance is apparent in cut shoots of tomato when grown in spore suspensions of the Fusarium and concluded that stem-localized anti-fusarial substances were important in resistance. Snyder *et al.* stated that field resistance to infection functions in the living cells of the root. Walker (1935), investigating resistance to wilt in the pea cultivar Alaska, considered that infection was prevented in resistant strains either because the root cortex lacked some essential nutrient or because it contained some inhibitory substance.

That exudates from roots can differentially affect the relative proportions of the rhizosphere microflora has previously been shown by many workers. For example, Katznelson, Rouatt & Payne (1954) found that amino-acids in root exudates from soybean, tomato and wheat stimulated the multiplication of certain rhizosphere-inhabiting bacteria. Timonin (1941) demonstrated the differential effects on rhizosphere fungi of by-products from roots of two flax cultivars. Although some recent studies of wilt resistance (Gottlieb, 1943; Irving, Fontaine & Doolittle, 1945) have emphasized the toxic effects on the pathogen of sap expressed from the stems and leaves of the host, it seems reasonable to consider that mechanisms localized in other parts of the plant may be important. In naturally

infected plants, the four phases of infection, growth in the rhizosphere, root invasion, growth through the root cortex and establishment in the vascular tract of the stem, could all meet with localized resistances, each important at particular stages of disease development. In peas, under suitable conditions, the selective action of root exudates would obviously preclude the need for other mechanisms of resistance elsewhere in the host.

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HELISCUS STELLATUS SP.NOV. AN AQUATIC HYPHOMYCETE

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(With Plate 7 and 2 Text-figures)

Heliscus stellatus is described from a submerged leaf of *Alnus glutinosus*. It has been grown in pure culture on nutrient agar. The morphology and behaviour in culture of *H. stellatus*, *H. longibrachiatus* and *H. aquaticus* are compared.

Heliscus stellatus sp.nov. (Pl. 7*a–o*; Text-fig. 1)

Fungus aquaticus submersus mycelio ramoso, septato. Conidiophora simplex vel paulum ramosa. Conidium (phialospora) hyalinum, unicellulare, consistens ex parte clavata quae prima oritur (2μ lata ad basim, ad 6μ apicem dilatata), circa 10μ longa, ex qua oriuntur tres projecturae conicae, 4μ latae ad basim angustatae ad apicem ad 1·5μ.

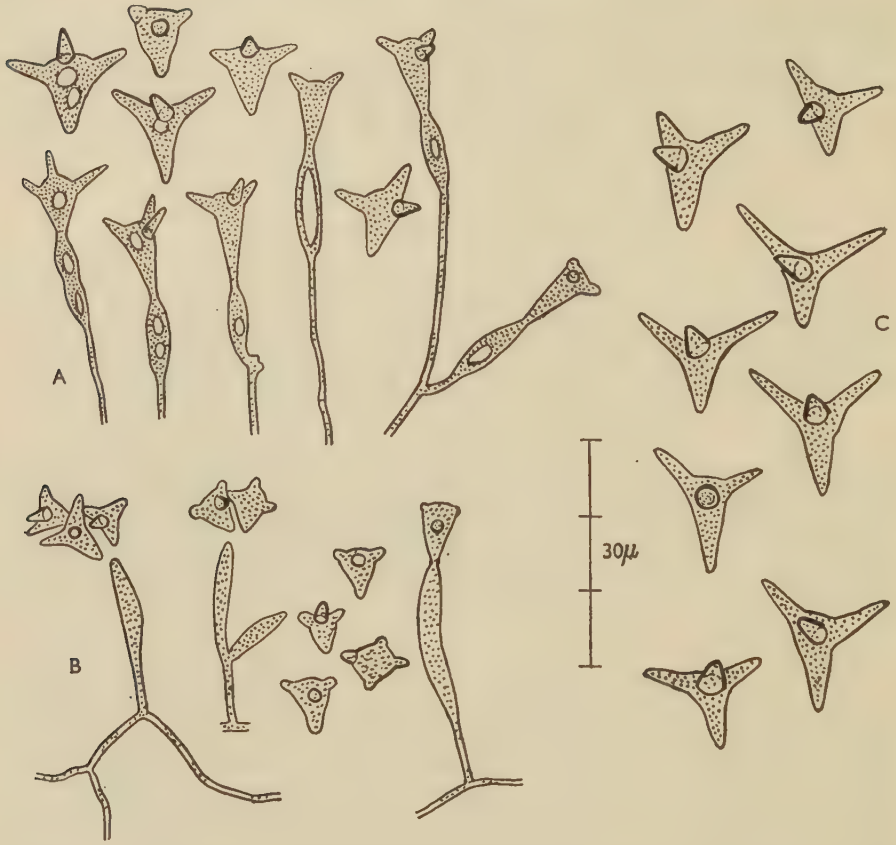
Hab. In foliis putrescentibus Alni in flumine jacentibus, Callow Green, Barton Broad, Norfolk, Anglia. Typus: Herb. I.M.I. 62078.

In October 1955 an undescribed species of *Heliscus* was found growing on a submerged decaying leaf from a freshwater ditch at Callow Green, Barton Broad, Norfolk. It was isolated in pure culture on nutrient agar.

In the original collection the conidiophores were mostly somewhat branched, each branch ending in a single phialide, but in culture they are usually unbranched. The unicellular, hyaline conidium (phialospore) consists of a first-formed main axis in the form of an inverted cone (about 2μ broad below widening to about 6μ above) from around the top of which there arise three conical arms 3–4μ wide at their insertion, but tapering to 1–1·5μ at their apices. The dimensions of each arm are not very different from those of the main axis, so that the whole spore is somewhat like a four-pointed star and this appearance has suggested the specific epithet.

Although the complete fungus has not previously been collected, unmistakable spores of this species have frequently been seen in samples of stream scum. A spore was figured by Ingold (1942; fig. 1, 20) and spores have recently been seen in abundance from a stream at Lullingstone, Kent, and from another at Ide Hill, Kent.

Two other aquatic species of *Heliscus* (*H. aquaticus* and *H. longibrachiatus*) have already been described (Ingold, 1942). In the stream spora both from Lullingstone and from Ide Hill all three species occur in some abundance in autumn, and for comparison photographs of the three are reproduced (Pl. 1). The spore of *H. stellatus* agrees with that of *H. longibrachiatus* in being unicellular, but the spore axis is more broadly cone-shaped and the conical arms arranged around the crown of the spore axis are quite different from the fine cylindrical arms of *H. longibrachiatus*. *H. aquaticus*



Text-fig. 1. *Heliscus stellatus*. A, spores and conidiophores from the alder leaf of the type collection; B, spores and conidiophores formed on nutrient agar; C, spores from Ide Hill stream spora.

with its 2-celled spore with short blunt arms, which are developed only under water, differs strikingly from the other two species.

A brief study has been made of *H. longibrachiatus* and *H. stellatus* growing on 2% malt agar and on Emerson's YpSs medium (Emerson, 1941) (Table 1). *H. longibrachiatus* was isolated from a submerged decaying alder

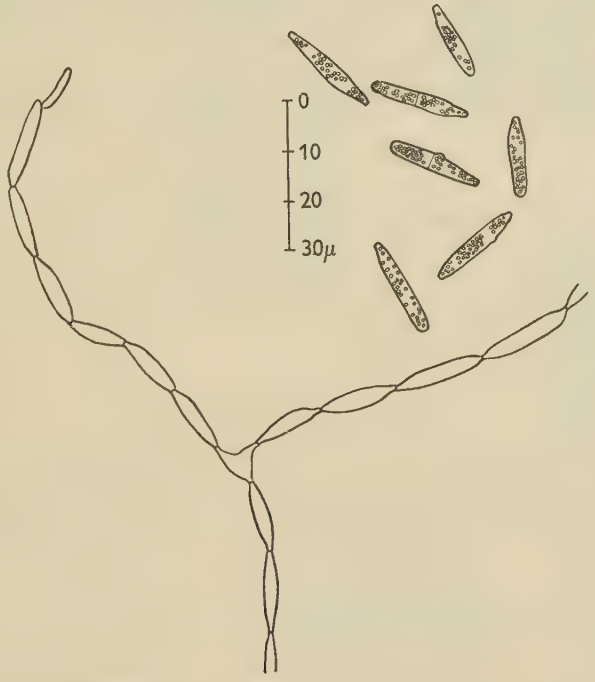
Table 1. *Comparison of* Heliscus longibrachiatus *and* H. stellatus *in culture*

Species	Medium	Colony diameter (mm.) After 7 days	Colony diameter (mm.) After 12 days
H. longibrachiatus	2% malt agar	2·3*	3·7
	YpSs medium	3·0	6·2
H. stellatus	2% malt agar	2·8	4·0
	YpSs medium	3·2	5·0

* Each figure gives the average diameter of three replicates. Cultures were grown at approximately 20° C.

leaf from a stream at Lullingstone. It has not previously been obtained in pure culture.

Both species grow very slowly in contrast to *H. aquaticus*, which grows more rapidly than any other aquatic Hyphomycete yet studied in culture. Ingold (1942) figures a 3-week-old colony grown on malt agar at 18° C. with an average diameter of 68 mm.



Text-fig. 2. *Heliscus longibrachiatus.* Monilioid aerial arthrospores produced on malt agar.

H. stellatus produces its characteristic phialospores on both malt agar and YpSs. In culture the phialides are not grouped together in sporodochia as they are in agar cultures of *H. aquaticus*. Cultures of *H. longibrachiatus* form no phialospores directly, but only after colony slices have been submerged in water for 1–2 days. Nevertheless, they do form branched aerial chains of monilioid arthrospores on both types of media (Text-fig. 2). No such spores have been seen in the other species. On mounting in water the arthrospores readily separate from one another. They are hyaline and mostly unicellular, although a few are 2-celled.

On malt agar *H. longibrachiatus* forms a dark grey colony with a very narrow white margin. *H. stellatus* also forms a dark grey colony, but the white margin is wider and there may be cream sectors. Both species are in sharp contrast to *H. aquaticus* in which the colony on malt agar is brown. However, in the two slow-growing species the colony is not always dark. Thus *H. longibrachiatus* forms a creamy-beige colony on YpSs and *H. stellatus* a pale grey one with a white margin.

Recently M. and Mme F. Moreau (1949) have considered an aquatic species of *Heliscus* which they identify as the type species, *H. lugdunensis*. However, it seems to us that the fungus they describe is very close to *H. aquaticus*. It may well be that only a single species is involved. M. and Mme Moreau consider that their fungus is closely akin to *Fusarium* and so far as *Heliscus aquaticus* is concerned we fully agree with them. However, neither *H. longibrachiatus* nor *H. stellatus* are in the least like *Fusarium* spp. Perhaps it may be necessary at a later stage to segregate these two species in a separate genus.

Our thanks are due to Prof. E. H. Warmington for his assistance with the Latin diagnosis.

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EXPLANATION OF PLATE 6

a–o, *Heliscus stellatus*. *a*, phialide from alder leaf bearing nearly mature spore; *b–d*, similar phialides from agar cultures; *f*, horizontal hypha bearing lateral conidiophores, two of which are branched; *g*, *h*, spores formed on agar cultures; *k–o*, spores from Ide Hill stream scum. *p*, *H. longibrachiatus*; spore from Ide Hill; *q*, *H. aquaticus*; spore from Ide Hill.

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(*Facing p.* 158)

Trans. Brit. mycol. Soc. **40** (1), 159–160 (1957).

BRITISH RECORDS, 13

13. **Puccinia arenariae** (Schum.) Wint. (*P. herniariae* Unger).

On 21 June 1956, specimens of *Herniaria ciliata* Bab., non Clairv., infected with a rust fungus, were collected in two separate localities on rock outcrops with short herbaceous cover between Downas Valley and Black Head, the Lizard Peninsula, Cornwall. The leaves of these plants were light yellow-green, upturned and slightly wilted. *H. ciliata* in Britain is restricted in distribution to the sea cliffs and coves from Polurrian Cove, near Mullion, to Coverack and surveys of this whole area in 1950, 1954 and 1955 failed to detect any infected specimens.

Microscopical examination of the small, dome-shaped, elliptical, dark purplish brown sori, which were abundant on the undersides of the stems, leaves and sepals, revealed teleutospores of a rust fungus. Measurements of the teleutospores (Table 1), the description by P. and H. Sydow in *Monographia Uredinearum* (1904) and comparison with material distributed by P. Sydow in Herb. Kew, all agreed with an identification as *Puccinia herniariae* Unger, *Ueber den Einfluss des Bodens*, etc., p. 218 (1836).

Table 1. *Teleutospore measurements of* Puccinia arenariae (P. herniariae) *on various* Herniaria spp.

Source of material ...	Herb. Reg. Kew		Herb. Gast. Genevier		France (D. Pigott)		Lizard (L. Frost)	
Host species ...	*H. glabra*		*H. latifolia*		*H. ciliata*		*H. ciliata*	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Teleutospore length (in μ)	32–43	36	25–43	37	32–41	36	29–43	34
Teleutospore width (in μ)	12–16	14	12–18	15	12–16	15	12–16	14

Sydow (1904) reported that *P. herniariae* had been recorded on stems and leaves of living *H. glabra*, *H. hirsuta* and *H. odorata* (a synonym of *H. polygama* J. Gay) in Germany, Austria, Denmark and Russia. According to these authors the very similar or identical rust, *P. montagnei* De Toni, had been reported on living leaves of *H. glabra* and *H. latifolia* in France. Guyot (*Uredineana*, **1**, 147, 150, 1939) listed records from Morocco of *P. herniariae* on *H. hemistemon* and of *P. montagnei* on *H. cinerea*. Hylander, Jørstad & Nannfeldt in Enumer. Ured. Scandin., *Opera Bot.* **1**, 37 (1953), using a wide species concept, placed *P. herniariae* Unger under *P. arenariae* (Schum.) Wint., of which they noted records on *H. glabra* L. in Denmark, Finland and Sweden, and on botanic garden material of *H. glabra* and *H. hirsuta* L. in Norway.

Wilson & Bisby (*Trans. Brit. mycol. Soc.* **37**, 61–86, 1954) do not list *P. herniariae* Unger or record *P. arenariae* (Schum.) Wint. as occurring on any species of *Herniaria* in their list of British Uredinales. Thus no rust fungus on any *Herniaria* species has hitherto been reported for Britain.

Scrutiny of the material in the Cambridge Herbarium over the range of distribution of *H. ciliata* (as given in *Flora of the British Isles*, 1952) revealed no specimens with rust from the Lizard or the Channel Islands. However, a specimen collected in July 1952 by Dr D. Pigott in short turf on the Pointe du Van, near Plogoff, Finistère, France, was heavily infected with the rust on the undersides of the stems, leaves and sepals. The host specimen appears to be very similar to the Lizard material and had been identified as *H. ciliata* Bab. by Dr Pigott (but see Blackburn & Adams, *Proc. bot. Soc. Brit. Isles*, **1**, 380, 1955). It would therefore appear that the Lizard material and possibly this specimen from France are the first reports of the rust on *H. ciliata*.

A specimen of *H. pyrenaica* J. Gay (a synonym of *H. latifolia* Lapeyr.) in the Cambridge Herbarium purchased in 1880 from the Herb. Gast. Genevier had been collected at Tamsarrieu and was found to be infected with this rust on the stems and leaves only. Measurements of ten teleutospores of this and the other specimens are given in Table 1.

Specimens have been deposited in the Cambridge (No. 74) and Kew Herbaria.

I wish to thank Dr N. F. Robertson for his assistance in identifying the rust and Dr S. M. Walters of the Cambridge Herbarium and Dr R. W. G. Dennis of the Kew Herbarium for supplying material.

L. C. FROST, Botany School (University of Cambridge)

1947–1956

1956 marks the Diamond Jubilee of the Society, 1957 that of the *Transactions*, and the Council decided that attention might appropriately be drawn to these anniversaries by bringing up to date the summary up to 1946 of the Society's history and the lists of forays, of honorary members, and of those who have served on the Council given in Volume 30 of these *Transactions*.

During the past decade there has been a marked increase in the membership (430 ordinary members in 1946, 650 in 1956). In spite of this gratifying growth, the Society's financial position gave the Treasurer cause for anxiety and necessitated increases in the subscription price of the *Transactions* in 1952 and in the membership subscription in 1953 and, because of steadily rising costs, a further increase in the price of the *Transactions* for 1957. However, these measures, generous benefactions from industrial organizations and assistance from the Government Grant-in-Aid of Scientific Publications administered by the Royal Society, have helped the Society to overcome the difficulties and the future if not rosy can for the time being be viewed with equanimity.

The *Transactions* have appeared regularly. The last two volumes have each averaged over a hundred pages more than pre-war volumes (a reflexion of the healthy state of British mycology) and in 1952 an Index (compiled by Dr G. R. Bisby) to the first thirty volumes was published.

The census sponsored by the Society of fungi recorded for Britain has been continued. Lists of agarics and boleti, together with Discomycetes, rusts and aquatic chytrids and of fungi pathogenic for man and higher animals have appeared in the *Transactions*, and further lists are in active preparation. Among occasional publications, a new edition of Sampson and Western's *Diseases of British grasses and herbage legumes* and Watson's *Census catalogue of British lichens*, both published in 1954, may be mentioned.

Since 1946 the pre-war pattern of Spring and Autumn Forays has been resumed and forays have been held in England, Wales, Scotland and Northern Ireland (and in 1957 Eire is to be visited), but an outstanding recent foray was that held in Normandy in 1952 in conjunction with the Societé Mycologique de France.

One innovation has been the formation of a library—primarily of taxonomic works and a number of mycological journals. The Society is grateful to all those members who have contributed to the library (which now comprises more than 400 volumes) and acknowledges a notable gift by the late Dr H. Wormald and the valuable bequests from Miss G. Lister and Mr A. A. Pearson.

Another innovation has been the issue, twice yearly since 1955, of a mimeographed News Bulletin.

One minor change in the administration of the Society is that the Secretary of the Plant Pathology Committee now ranks with the Secretary of the Society and the Foray Secretary as an officer. Since 1954 the number of Honorary Members of the Society at any one time has been limited to twelve. Reduced subscriptions have been conceded to retired members of the Society of more than 25 years' standing.

PAST-PRESIDENTS AND OTHER OFFICERS, MEMBERS OF THE COUNCIL AND HONORARY MEMBERS, TOGETHER WITH LISTS OF THE AUTUMN AND SPRING FORAYS 1947–1956

Presidents

Chesters, C. G. C.	1947	Pearson, A. A.	1952
Muskett, A. E.	1948	Ingold, C. T.	1953
Findlay, W. P. K.	1949	Garrett, S. D.	1954
Ainsworth, G. C.	1950	Hawker, Miss L. E.	1955
Gregory, P. H.	1951	Graddon, W. D.	1956

Elected Vice-Presidents

Duncan, J. T.	1947	Moore, W. C.	1952
O'Connor, P.	1948	Hickman, C. J.	1953
Preston, N. C.	1949	Graddon, W. D.	1954
Wilkins, W. H.	1950	Howard, H. J.	1955
Sowter, F. A.	1951	Hora, F. B.	1956

After their year of office, Presidents serve for a further two years as Vice-Presidents.

Secretaries

Ainsworth, G. C.	1942–7	Webster, J.	1953–
Hickman, C. J.	1948–52		

Foray Secretaries

Ainsworth, G. C.	1948–9	Hora, F. B.	1953–6
Smith, G.	1950–2		

Plant Pathology Committee Secretaries

Croxall, H. E.	1946–9	Batts, C. C. V.	1952–4
Moore, Miss F. J.	1950–1	Hirst, J. M.	1955–

Treasurer

Buddin, W. 1947–

Editors

Moore, W. C.	1946–51	Ainsworth, G. C.	1952–
Gregory, P. H.	1950–5	Garrett, S. D.	1956–

Elected Members of the Council

Croxall, H. E.	1946–8	Gregory, P. H.	1949, 1956–
Hughes, S. J.	1946–8	Waterhouse, Miss G. M.	1949–51
Sowter, F. A.	1946–8	Wood, R. K. S.	1949–51
Graddon, W. D.	1947–9	Brooke, J.	1950–2
Foister, C. E.	1947–9	Hora, F. B.	1950–2
Hickman, C. J.	1947	Moore, Miss F. J.	1950–2
Bond, T. E. T.	1948–50	Robertson, N. F.	1950–2
English, Miss M. P.	1948–50	Orton, P. D.	1951–3
Smith, G.	1948–50	Storey, I. F.	1951–3
Wallace, E. R.	1948–50	Webster, J.	1951–2

Ellis, M. B.	1952–4	Manners J. G.	1954–6
Topping, Mrs M. P.	1952–4	Plunkett, B. E.	1954–6
Batts, C. C. V.	1953–5	Brown, Miss A. H. S.	1955–
Brian, P. W.	1953–5	Reid, D. A.	1955–
Duddington, C. L.	1953–5	Savory, J. T.	1955–
Palmer, J. T.	1953–5	Fraymouth, Miss J.	1956–
Smith, G.	1953–4	Wallace, T. J.	1956–
Colhoun, J.	1954–6		

Honorary Members

Barnes, B.	1950–	†Maire, R.	1939–49
†Brooks, F. T.	1948–52	Moore, W. C.	1951–
Buddin, W.	1954–	†Pearson, A. A.	1946–54
Dodge, B. O.	1946–	†Petch, T.	1941–8
†Falck, R.	1946–55	Ramsbottom, J.	1945–
Gäumann, E.	1946–	Swanton, E. W.	1947–
Heim, R.	1946–	Wakefield, Miss E. M.	1941–
†Lister, Miss G.	1924–49	Watson, W.	1951–

† Deceased.

Lists of members of the Society were published in the *Transactions*, Vols. **33**, **36**, **38**.

Forays

	Spring	Autumn
1947	Reading, Berks.	Exeter, Devon
1948	Flatford Mill, Suffolk	Belfast, Northern Ireland
1949	Lincoln	Oxford
1950	Totnes, Devon	Bangor, Wales
1951	Marlborough, Wilts.	Hereford
1952	Perranporth, Cornwall	Le Mans, France
1953	Juniper Hall, Surrey	Dunkeld, Scotland
1954	Windermere, Westmorland	Southampton, Hants.
1955	Tring, Herts.	Bristol, Glos.
1956	Flatford Mill, Suffolk	Sheffield, Yorks.

PROCEEDINGS

MEETINGS

Meeting held in the Botany Department, University of Nottingham, at 2.0 p.m., 28 July 1956. Professor C. G. C. Chesters in the chair.

G. J. F. Pugh. Observations on the fungal flora of the leaf litter of *Carex paniculata*.

Collections were made from four zones in the leaf litter of *Carex paniculata*: outer leaves, distal ends; outer leaves, proximal ends; inner leaves, around the core of the tussock; and from the interior of the tussock.

Fungi found directly included *Metasphaeria cumana*, which was the most common Ascomycete, three species of *Leptosphaeria*, *Chaetomium globosum* and *Sordaria macrospora*. Sterile mycelium resembling that of *Metasphaeria* was isolated from surface sterilized leaves which were still living. Members of the Fungi Imperfecti included: Sphaeropsidales: *Ascochyta sodalis*, *Coniothyrium* sp., *Diplodina caricis*, *Pycnothyrium junci*, *Stagonospora paludosa*; Moniliaceae: *Botrytis cinerea*, *Cephalosporium acremonium*, *Trichoderma viride*; Dematiaceae: *Acremoniella verrucosa*, *Alternaria tenuis*, *Cladosporium herbarum*, *Helminthosporium biforme*, *Periconia paludosa*, *Tetraploa aristata*; Stilbaceae: *Sporocybe rhopaloides*, *Stysanus stemonites*.

Most of the work was done on surface-sterilized leaf portions from the four collecting zones. The greatest number of isolations and of species was obtained from the distal ends of the outer leaves. The numbers showed a progressive decrease in the proximal ends of the outer leaves, the inner leaves and the interior of the tussock. *Penicillium spinulosum* was the most frequently isolated species. It was dominant in the proximal ends and in the inner leaves. Other common species included *Fusarium culmorum*, which was dominant in the distal ends, *Cladosporium herbarum*, species of *Cephalosporium*, species of *Mucor*, *Penicillium citrinum*, *P. corylophilum*, *P. notatum*, and *Trichoderma viride*, which was dominant in the interior of the tussock.

There was a definite seasonal variation in the numbers of isolations of these fungi, with a period of great activity in the summer months. The most active fungi in the summer were *C. herbarum*, *F. culmorum* and species of *Penicillium*.

The main environmental factors found to influence this seasonal variation in numbers of isolations were temperature and the water content of the substrate.

M. Brook. Tetrachloronitrobenzene as a fungicide.

Dusts containing 2356-tetrachloro-1-nitrobenzene can be used to control *Botrytis* disease of lettuce. When a dust containing 5% of TCNB was used on lettuce (May King) grown in unheated dutch lights from autumn to spring 1952–3 and during 1953–4, it produced significant increases in the survival of treated plants when 25–50% of the untreated plants died from disease. Protection from disease was accompanied by a check to growth. When the rate of application did not exceed $\frac{1}{4}$ oz./sq.yd. the growth check was slight and on balance the treatment was worth while. When more than $\frac{1}{4}$ oz./sq.yd. was used the delay in reaching maturity could nullify the advantage gained by reducing loss from disease.

To avoid the local variations in deposit which inevitably occur when the soil surface of a glasshouse is dusted, it is recommended that the TCNB should be discharged from a smoke generator. When this method of application can be used it ensures even distribution of the fungicide.

Tetrachloronitrobenzene is also used to control Dry Rot disease of potatoes caused by *Fusarium caeruleum*. The 2356-isomer will retard the production of sprouts, and the yield of treated tubers may be reduced, or may contain an increased proportion of small tubers. Laboratory experiments, followed by field experiments from 1952 to 1955, using

six varieties of potatoes, showed that the asymmetrical isomer, 2345-tetrachloro-1-nitrobenzene, was a better fungicide than the 2356-isomer (although the difference was not quite significant at $P = 0{\cdot}05$), and it did not retard the sprouting of the treated tubers. Yields from 2345-TCNB-treated seed were not reduced and did not contain more small tubers than those from untreated seed. In these experiments the chemicals were usually used as 5% dusts at the rate of 5 lb. to a ton of potatoes. Maximum protection from disease was obtained if they were applied as the tubers were lifted.

The 2345-isomer checks the growth of lettuce more than the 2356-isomer does, and it is not so effective for the control of *Botrytis* disease.

M. Dransfield. The effects of tetrachloronitrobenzene on the soil microflora.

TCNB is phytotoxic to lettuce as well as being fungistatic towards *Botrytis cinerea*, and so it might possibly affect other organisms. Dilution plates prepared from soils dusted with 5% TCNB at ½ oz./sq.yd. showed no significant alteration of the microflora, but when the fungicide was thoroughly mixed with the soil at ten times the normal rate the numbers of fungal species were slightly reduced, although the commoner soil fungi were unaffected.

There was a sharp drop in the number of species isolated on Warcup plates prepared from soils treated with TCNB at ten times the normal rate; there was no effect at the normal rate of application. 2356-TCNB was more inhibitory than the 2345-isomer, but neither affected species of *Pythium* or of *Mortierella*. Although the fungicide somewhat inhibited *Arthrobotrys oligospora*, its predatory ability was unaffected.

The high rate of damping-off among lettuce seedlings treated with TCNB was shown to be due to the resistance of lettuce to *Pythium* attack being reduced by the fungicide, and not to an increase of *Pythium* in the soil.

The use of the percolation apparatus for daily sampling of treated soil was described, and its drawbacks for isolating fungi were mentioned. The numbers of fungi were somewhat reduced in soils treated with TCNB above ten times the normal rate, but bacteria were markedly increased. It was shown that the numbers of amoebae bore an inverse relationship to those of bacteria. A reduction of both the symbiotic and non-symbiotic nitrogen-fixation bacteria was demonstrated for both isomers of TCNB when applied at well over the normal rate; the 2356-isomer produced the more severe effect.

It was concluded that although TCNB can be made to affect the microflora when applied at an abnormally high rate, there is no effect when it is applied at rates which control grey mould without being phytotoxic to lettuce.

C. L. Duddington. Predaceous fungi and the biological control of nematodes.

Predaceous fungi are common in soil and in decaying vegetable matter generally. The first serious attempts to use them for eelworm control were made by Linford and his co-workers in Hawaii, working on pineapple root-knot eelworm. Soil inoculation experiments gave poor results, but it was found that the addition of fresh plant material to the soil acted as a stimulant to the naturally occurring predaceous fungi, with a concomitant reduction in the numbers of infective *Meloidogyne* juveniles. The Hawaiian work ceased shortly before the outbreak of the 1939 war, and has not been resumed.

During the war, experiments were carried out in France, mainly on the small nematodes that attack man and domestic animals. It was shown that the predaceous fungi could capture and kill these nematodes, and methods for culturing the fungi in bulk were devised. The work apparently ceased in 1945.

During the last five years, work has proceeded in this country, mainly on the control of cyst-forming species of *Heterodera*, such as the potato root eelworm. It has been found that the effectiveness of the fungi as agents of eelworm control is closely bound up with the organic matter in the soil, and Linford's observations on the effect of adding plant material have been confirmed for cereal root eelworm in oats. Pot and field experiments have shown that, given the right conditions, potato root eelworm, cereal root eelworm, and pea root eelworm can be controlled by the use of predaceous fungi, though more work remains to be done before their use becomes general.

Meeting held at Birkbeck College, London, W.C. 1 at 11.0 a.m., 12 October 1956. The President, Mr W. D. Graddon, in the Chair.

Mycology and Forestry

M. Wilson. Introduction.

T. R. Peace. The control of diseases in the forest.

Control of diseases in the forest nursery is essentially a similar problem to that posed by agricultural and horticultural crops, but control in the forest is an entirely different one. The large areas involved, the often difficult terrain, and the height and density of the crop, all make the use of standard control measures very difficult. In addition, the long period for which one crop occupies the ground, and the comparatively low value per acre per year, make expensive and particularly repetitive, treatments virtually impossible.

It is necessary, therefore, to base control in the forest largely on indirect methods. For new plantings, choice of existing species, variety or clone, breeding for disease resistance, and choice of site are all possible disease-avoiding actions. For established crops adaptions of normal silvicultural treatments must be tried, for instance frequent cutting of an alternate host, which ranks as a weed species, cutting off lower branches (brashing) at times of year when fungal infection is least likely to occur, removing diseased trees in the course of normal thinning of the crop, and, in the case of *Rhizina inflata*, associated with 'Group dying' of conifers, restricting fires lit in the forest to special sites.

In a few instances direct action may be justified. Based on the high value of the timber, eradication on a limited basis is in operation for Watermark disease of cricket-bat willow (*Bacterium salicis*); but it is considered that eradication is seldom possible or even desirable with other tree diseases. Fungicidal treatment of thinning stumps, which is very cheap, is in use to prevent spread of *Fomes annosus* by stump infection. On a limited scale, where the trees to be protected have a special value, for instance in arboreta or in seed orchards of selected tree strains, trenching can be tried to prevent the spread of root fungi. Experiments are now in progress to test the possibility of treating one crop of trees, at or just before felling, to prevent the continuation of root fungus infection, in particular of *Fomes annosus*, into the succeeding crop.

R. G. Pawsey. The overwintering of *Keithia thujina**, the causal agent of cedar leaf blight.

In Great Britain, *Keithia thujina* causes a serious leaf blight in nurseries of *Thuja plicata*, the Western red cedar. In mature stands the disease is not of economic importance. On nursery plants the chief symptoms are browning of the foliage followed by growth check and often extensive die-back. The fungus does not spread from leaf to leaf, and does not penetrate into the vascular tissue.

Apothecia are formed on infected leaves from early May until November, but usually occur in greatest number at the beginning and end of this period. No imperfect stage of *Keithia* has been observed. Until recently the condition in which the fungus overwintered was unknown.

At intervals during the winter of 1955–6 infected plants were taken from a nursery and potted in a warm greenhouse. Careful examination of infected plants in the nursery showed that small pustulate structures were often associated with old infected brown leaves. In the greenhouse all the lesions on a number of branches were briefly described, plotted and any changes with time followed. It was definitely shown that after about 3 weeks the pustulate structures developed into mature apothecia from which ascospore discharge took place. The pustules were incipient apothecia, and infrequently young asci were observed between the paraphyses.

After about 6 weeks in the greenhouse severe new infection was produced on the plants. This also occurred in two experimental nurseries at the beginning of May 1956.

* The generic name *Keithia* Sacc. has been superseded by *Didymascella* Maire & Sacc., but the former is invariably used by forest pathologists.

In these nurseries old infected plants were intermixed with uninfected plants but the new heavy infection was confined entirely to the previously infected plants. It appeared then that the ascospores discharged from mature apothecia which had overwintered in the incipient stage were not responsible for this outbreak.

Other evidence indicated that ascospores overwintering on the surface of, or in crevices between, leaves were the primary cause of the spring infection.

J. G. Manners. Modes of canker production in European larch.

J. Rishbeth. *Fomes annosus* on stumps.

An experiment set up in 1947, in which stumps produced during the first thinning of pines were treated in various ways, shows excellent agreement between the number of trees now dying and the proportion of stumps infected with *Fomes annosus*, as determined by the treatments. In plots with the highest natural stump infection, treatment with paint or creosote was 97% effective against killing, and the average effectiveness of these treatments in the whole experiment was 86%.

A recent survey of large-scale stump creosoting in Thetford Chase indicates that its effectiveness varies and is sometimes lower than in the experiment quoted; the probable reasons for this are discussed. During the survey further evidence came to light of the effect of weather on stump infection: thus the severe drought in July 1955, caused a sharp drop in stump infection by *Peniophora gigantea* and a marked rise in that by *Fomes annosus*. Observations showed that spore production by the latter fungus was little affected by the drought.

With current losses in East Anglian pine plantations averaging nearly 7% at the second thinning, it is important to investigate stump treatment further. Early stages of fungal succession in stumps are largely determined by the outcome of competition between species colonizing the cut surface. The mode of action of protectants is at present little understood, but there are many possibilities, including (1) exclusion of all fungi from the stump surface, and later colonization by other means, (2) microflora selected on the basis of relative tolerance to the protectant, with the woody substrate little changed, and (3) widely varied microfloras resulting from alterations to the substrate. In practice, such effects are probably combined in various ways but situation (1) occurred to some extent in the first experiment quoted and situation (2) is probably common in the current creosoting. Situation (3) has arisen in experimental treatments: thus *Trichoderma viride* regularly becomes dominant in stumps treated with 40% ammonium sulphamate and *Botrytis cinerea* in stumps treated with sodium chlorate. The former treatment may prove useful for treating stumps of trees suffering root infection with *Fomes annosus* and possibly those of trees infected with other root parasites, such as *Armillaria mellea*.

S. D. Garrett. The indirect effect of soil fumigation on *Armillaria mellea*. See *Canad. J. Microbiol.* 1957 (in the Press).

J. L. Harley. The ecology of tree mycorrhiza.

The forest trees, which form ectotrophic mycorrhiza are dual organisms in natural habitats, in the same sense that lichens are dual organisms. The infection is not obligate to the host except in an ecological sense. The intensity of infection depends, particularly, in inverse measure, upon nutrient availability and in direct measure upon light intensity and photosynthesis. The interaction of light intensity and mineral supply upon root growth and root competition in forests, together with the effects of these factors on mycorrhizal development point to the complexity of the problems which may be worth the consideration of foresters and ecologists.

The outstanding defects in knowledge of mycorrhizal fungi are in the lack of information on their activities apart from the root. Their lack of close specificity also poses problems concerning the relative efficiency in absorbing functions of mycorrhizas formed by different fungi with one host species. The recent demonstration that spores are efficient as infective propagules indicates that in most European forest sites unhealthy

growth, together with lack of mycorrhizas, are likely to be overcome by soil treatment rather than inoculation.

The stimulus which selects mycorrhiza fungi to become dominant on the host roots is becoming more clear. Internal high carbohydrate status and root secretions play a part but as yet no morphogenic substance encouraging fungi to form pseudo-parenchymatous tissue is known. The morphogenic effects of the fungi on their hosts has been studied and auxins play their part in the process, the net result of which is the prolongation of the life and complexity of short roots. Nevertheless, mycorrhizas function for short periods only, e.g. 8 months or little more in beech, and are replaced repeatedly by branching of the permanent root axes.

There is no doubt that on podsols and brown-earth soils mycorrhizas in the humic layers function as efficient absorbing organs and that seedlings experimentally deficient in them, grow less vigorously than their infected counterparts. This is partly explicable in terms of root form, but the presence of a fungal sheath with external hyphae confers on mycorrhizas properties of their own. Nutrients pass into the hyphae and fungal sheath and thence to the host. Laboratory experiments with excised mycorrhizas have shown that these organs are efficient aerobic salt-absorbing mechanisms, which exercise selection on the ions absorbed. Although the primary site of accumulation may be in the sheath, the whole organ competes efficiently with fungal, microbial and higher plant denizens of the humus layers. There is evidence of a translocating mechanism dependent upon temperature and oxygen supply which brings about the onward movement of accumulated salts, especially phosphate, to the host tissue.

It seems likely that tree seedlings, except new exotics, transplanted to forest sites in forestry practice will become mycorrhizal where these sites are suitable for tree growth. It is an important forestry problem to decide what kind of root-system, mycorrhizal or non-mycorrhizal, is best suited to lifting, carriage and transplantation.

THE FLATFORD MILL FORAY

24–28 May 1956

By F. B. HORA, *Foray Secretary*

For this, the twenty-seventh Spring Foray, members were accommodated at Flatford Mill and the adjoining Willy Lott's cottage, East Bergholt, Suffolk, both well known for their association with John Constable, the painter, whose father once owned the Mill. About twenty members were present.

On the first day (Thursday), a circular trip was made taking in Hollesley Heath, Shingle Street (on the coast) and Staverton Thicks. On Friday morning, by kind permission of Lady Wake Walker, we visited the woods on her estate. A lane divides these woods: that part on the side remote from the house is known as Commons Wood and on the near-side as Tree Meadows Wood. (Records in the List of Species are sometimes given in terms of these divisions.) On the same afternoon, a party went to Fishpond Wood, which is close-by. On Saturday, Stour Wood was searched, and Dodnash Wood on Sunday morning.

Weather conditions during the Foray were dry and often bright and sunny—in fact, a continuation of conditions prevailing during preceding weeks. An abundance of material was not, therefore, to be expected. This is the main cause of the shortness of the List of Species, but in addition it should be pointed out that some of the fungus groups lacked workers who are specialists in those groups. Nevertheless, some interesting finds were made. *Phellinus torulosus* has only so far been recorded for the British Isles from Killarney on a dead stump of *Arbutus unedo* (these *Transactions*, **35**, 35 (1953)). This tree is part of the Hiberno-Lusitanian group and it is interesting to note that the Flatford gathering was from sweet chestnut, a naturalized but nevertheless introduced tree with an extensive southerd European distribution like *Arbutus*. Mr Graddon was again very pleasen to have a further locality for *Sclerotinia hirtella* which had turned up in some quantity at the previous Spring Foray. *Coprinus lagopides* was definitely identified. Carleton Rea did not claim to have found it, and described it as rare. It is probably quite common, but passed over in mistake for *C. lagopus*, from which it is at once separated by having subglobose spores as distinct from elliptic ones.

Our warmest thanks are due to the Warden of Flatford Mill, Mr John Bingley, and to his staff, for making our stay at the Mill so pleasant.

For help in preparing this report it is a pleasure to thank Dr Agnes Brown, Messrs Finney, Fletcher, Graddon, Parker-Rhodes, Reid and Stenton. I am especially grateful to Dr Parker-Rhodes who not only supplied most of the records for resupinates, but also put his extensive knowledge of the area at our disposal. The accompanying List of Species is along the usual lines. For nomenclature, see these *Transactions*, **38**, 185 (1955).

List of Species

C. = Commons Wood (Wake Walker estate); *D.* = Dodnash Wood; *F.* = Flatford Mill; *FP.* = Fishpond Wood; *H.* = Hollesley Heath; *SS.* = Shingle Street; *ST.* = Staverton Thicks; *T.* = Tree Meadow Woods (Wake Walker estate); *W.* = Wake Walker estate. *Notes*: (1) chestnut refers to the sweet chestnut, *Castanea sativa*; (2) voucher material of the Hyphomycetes is deposited at the Commonwealth Mycological Institute.

MYXOMYCETES

Lycogola epidendrum, *F.*
Reticularia lycoperdon, *F.*
Trichia persimilis, *F.*; scabra, *D.*; verrucosa, *F.*

EU-ASCOMYCETES

Pyrenomycetes

Chaetosphaeria annumera, on rotten wood, *T.*
Epichloe typhina, on *Poa trivialis*, *D.*
Erysiphe graminis, on *Poa trivialis*, *D.*
Gloniopsis levantica Rehm, on rotten wood, *T.*
Hypomyces aurantiacus (conidial), on *Polyporus*, *H.*, on rotten wood, *D.*
Hypoxylon multiforme, *ST.*, serpens, *ST.*
Lophiotrema praemorsum, on *Rubus*, *SS.*
Xylaria hypoxylon, *D.*

Discomycetes

Aleuria repanda.
Ascobolus cruani.
Ciliaria setosa, *D.*
Dasyscypha brevipila; palearum (Desm.) Massee; virginea.
Hyaloscypha dematiicola (B. & Br.) Nannf., on chestnut, *S.*, *T.*; hyalina agg.
Ombrophila clavus, *W.*; verna, *W.*
Orbilia sp., on dead wood, *F.*
Phaeobulgaria inquinans (Fr.) Nannf.
Phialea cyathoidea (Fr.) Gill.
Rutstroemia echinophila.
Sclerotinia hirtella, on chestnut debris.

HETERO-BASIDIOMYCETES

Auriculariales

Auricularia auricula-judae, on elder, *D.*, *SS.*; mesenterica, on dead logs, *F.*
Platygloea vestita, on rotten chestnut, *S.*

Tremellales

Sebacina fugacissima, on birch, *ST.*

Uredinales

Phragmidium fragariastri, on *Potentilla sterilis*, *S.*; violaceum, on *Rubus fruticosus* agg., *S.*, *W.*
Puccinia adoxae, on *Adoxa moschatellina*, *D.*; caricina, on *Urtica dioica*, *Carex acuta*, *S.*, *W.*; malvacearum, on *Malva* sp., *W.*; menthae, on *Mentha aquatica*, *W.*; obtegens, on *Cirsium arvense*, *F.* (river bank), *S.*; phragmitis, *SS.*, on *Rumex crispus*, *F.* (river bank); pulverulenta, on *Epilobium hirsutum*, *F.*, *FP.*, *W.*; taraxaci, on *Taraxacum officinale*, *W.*; violae, on *Viola canina* agg., *S.*

Tranzschelia anemones, on *Anemone nemorosa*, *S.*
Uromyces ficariae, on *Ranunculus ficaria*, *D.*, *W.*; poae, on *R. ficaria*, *W.*; rumicis, on *Rumex crispus*, *W.*; scillarum, on *Endymion non-scriptus*, *W.*, *SS.*

Ustilaginales

Urocystis agropyri, on *Agropyron* sp., *SS.*; anemones, on *Anemone nemorosa*, *S.*
Ustilago longissima, on *Glyceria maxima*, *F.*, on *G. fluitans*, *FP.*; violacea, on *Silene maritima*, *S. cucubalis*, *SS.*, on *Melandrium rubrum*, almost everywhere.

HOMO-BASIDIOMYCETES—Hymenomycetes

Aphyllophorales

Caldesiella ferruginosa (Fr.) Sacc., on ash branch, *S.*
Coniophora betulae (Schum.) Karst., *W.*, on chestnut, *D.*
Corticium comedens, on oak, *T.*; confine, on pine log, *H.*; sambuci, on pine logs, *H.*, on elder, *D.*, *W.*; seriale, *T.*; vagum, on oak, *C.*, *T.*
Daedalea confragosa, on birch branches, *D.*, on chestnut branches, *S.*; quercina, on chestnut stumps, *S.*; unicolor, on sycamore, *FP.*
Fomes ferruginosus, on birch sticks, *ST.*, *F.*, *FP.*
Gloecystidium lactescens (Berk.) v. H. & L., on chestnut, *D.*; pallidum (Bres.) v. H. & L., on rotten birch, *ST.*, on alder branch, *C.*; praetermissum, Bres., on elm stick, *SS.*
Grandinia farinacea, on chestnut, *S.*, *W.*; helvetica, on birch log, *ST.*; microspora, *T.*
Hymenochaete cinnamomea, on alder sticks, *C.*; corrugata, on alder sticks, *C.*; rubiginosa, *W.*, on alder branches, *C.*, on chestnut, *S.*, on chestnut stump, *D.*
Hypochnus sphaerosporus, on pine log, *H.*
Lenzites betulina, on birch stump, *S.*
Merulius himantioides, on pine log, *S.*
Mucronella aggregata, on rotten birch, *ST.*
Odontia crustosa, on elm logs, *D.*
Pellicularia (Bres.) Rogers, on wood, *D.*; sub-coronata (v. H. & L.) Rogers, on birch log, *ST.*, on elm, alder, *C.*
Peniophora hydnoides, *W.*, on chestnut, *S.*; laevis, on rotten birch, *ST.*, on birch bark, *D.*; leprosa, on oak branch, *C.*, on chestnut, *S.*; lithargyrina Bourd. & Galz., on ash log, *F.*; nuda, on ash branch, *D.*; pallidula, on birch, *ST.*; pubera, on elm stick, *SS.*, on rotten birch, *D.*; subulata Bourd. & Galz., *H.*; violaceolivida, on chestnut, *S.*
Phellinus torulosus (Pers.) Bourd. & Galz., on chestnut stump, *D.*
Polyporus adustus, *D.*; betulinus, on birch logs, *ST.*; hispidus, on elm, *FP.*; radiatus, on alder branches, *C.*; schweinitzii, on pine stump, *H.*; squamosus, on elm stump, *Flatford Lane*; sulphureus, on chestnut logs, *S.*
Polystictus abietinus, on pine log, *S.*; pubescens, on oak branch, *T.*; versicolor, *C.*, on pine log, *H.*, on chestnut logs, *S.*
Poria lenis Karst., on chestnut log, *S.*; versiporum, *W.*, on ash stick, *SS.*, on birch log, *ST.*, on alder sticks, *C.*, on chestnut, *S.*, on various substrates, *D.*; vulgaris, on chestnut, *S.*
Stereum hirsutum, on birch, *D.*, *ST.*, on oak, *C.*, *F.*; purpureum, on birch log, *D.*; rugosum, on chestnut, *D.*

Agaricales

Coprinus lagopides, *D.*; radians, on holly, in contact with *Ozonium*, *ST*
Hypholoma fasciculare, on oak stump, *T.*
Mycena acicula, *D.*; galericulata, *D.*; speiria, *D.*
Omphalia fibula *var.* swartzii, *D.*
Pholiota aegerita, on elm stump, *Flatford Lane*; praecox, on stump, *FP.*
Pleurotus cornucopiae, on holly, *ST.*
Pluteus cervinus, *D.*, on birch log, *ST.*
Psathyrella obtusata *sensu* Lange, *S.*

HOMO-BASIDIOMYCETES—Gasteromycetes

Phallus impudicus (egg stage), under oak, *ST.*

FUNGI IMPERFECTI

Hyphomycetes

Botrytis cinerea, on chestnut, *S.*
Brachysporium apicale, on chestnut, *S.*, *T.*; britannicum Hughes, on wood, *T.*
Haplaria grisea, on rotten wood, *T.*, on holly, *ST.*
Helminthosporium simplex, on rotten wood, *T.*
Monotospora sphaerocephala, on *Acer*, *T.*
Oidium aureum Fr., on holly, *ST.*
Paecilomyces elegans (Corda) Mason & Hughes, on *Acer*, oak, *T.*
Papularia sphaerosperma, on *Phragmites*, *SS.*, on *Sambucus*, *D.*
Penicillium thomii, on rotten wood, *T.*
Podoconis alta (Preuss) Mason & Hughes, on alder, *D.*
Trichoderma viride, on *Phragmites*, *SS.*, on sycamore, *T.*
Verticillium cyclosporum (Grove) Mason & Hughes, on rotten wood, *Alnus*, *T.*, on birch, *ST.*

THE THIRTIETH ANNUAL PLANT PATHOLOGY FIELD MEETING

27–28 July 1956

Over forty members attended this meeting in the Nottingham district. Accommodation was provided in the Halls of Residence of the School of Agriculture, University of Nottingham, Sutton Bonington. Members were welcomed by Prof. F. L. Milthorpe, and then shown agronomic studies of the development of the potato crop, after which Mrs N. McDermott gave an entertaining and instructive demonstration of the collection of potato varieties and the rogue and virus collections. The glasshouses of the Agricultural Sciences and Horticultural Departments were visited to see work on the effects of soil moisture and salt content on the growth and health of tomatoes; control of the development of raspberries, by manipulation of the temperature and photoperiod; studies of the competition between crop plants and weeds, both above and below soil level; plant nutrition, and various methods for measuring solar radiation. After lunch Dr Hudson described the plant growth rooms of the Horticultural Department, and members then visited demonstrations dealing with potato diseases and sprout depression, prepared by the Potato Storage Investigation Unit of the Agricultural Research Council; seed germination; aphis infestation of crops; choke of grasses and *Mycosphaerella* ring spot of crucifers.

The morning of the second day was spent visiting the Lenton Experimental Station of Boots Pure Drug Company. The methods used in the laboratories, glasshouses and field for screening compounds for activity as fungicides, insecticides or acaricides were described. Members saw trials used to distinguish phytotoxicity from the symptoms on a variety of crop plants resulting from deficiencies of pairs of elements. In commercial scale glasshouses, experiments were in progress on various rooting media and irrigation methods for tomatoes and carnations. Here as elsewhere in the station members were impressed by the very high standards of cultivation which they saw.

After lunch, Prof. C. G. C. Chesters took the chair at a meeting in the Botany Department of the University (see p. 164). In conclusion, Dr Hickman expressed the thanks of the visitors to all their hosts, to the speakers and to those who had arranged demonstrations, and in particular to Dr Pugh the local secretary for the very successful organization of the meeting which all had enjoyed.

J. M. HIRST

Secretary, Plant Pathology Committee

REVIEWS

A Revision of the British Helotiaceae in the Herbarium of the Royal Botanic Gardens, Kew, with notes on related European species. By R. W. G. Dennis. (Mycological Papers, No. 62. Commonwealth Mycological Institute, Kew, 1956.) Pp. 216, 1 plate, 179 text-figures. Price: 60*s*.

This volume contains detailed descriptions—many drawn up from type material—of 190 species of Helotiaceae, 11 species tentatively assigned to *Calycellina* von Höhnel and 28 species placed by Karsten in *Helotium* and now excluded therefrom by the author. The work is arranged mainly according to Nannfeldt's system (1932), and the studies of Whetzel on Sclerotiniaceae and of White on *Rutstroemia* are incorporated. Generic and specific keys are provided and in these the structure of the excipulum frequently figures; clearly, for success in identification, the preparation of a good median section of the specimen must be accepted as an essential step. Line drawings showing the excipular structure in section, the hymenium details and the fungus habit are freely inserted in the text throughout the book. Abundant critical taxonomic notes run through the work as an illuminating thread revealing, on the one hand, the wide field penetrated by the author's studies and, on the other, the considerable scope for further work. The difficulties of generic delimitation are emphasized and future work on fresh collections may well lead to modifications of the author's scheme; nevertheless, provisional though it may be, it provides a valuable present guide through the labyrinth. Each description is followed by a list of the collections at Kew and here we see how few species have been widely collected and how many deserve further seeking. A useful host index precedes the index proper; the latter, based on generic names, appears adequate but, for a group so rich in synonymy, an index of specific epithets would have been a welcome addition. With this volume Dr Dennis makes another valuable contribution to Discomycete literature and brings order into a realm hitherto chaotic. Moreover, he provides a hand-book which should enable us to identify accurately many of the Helotiaceae we may collect. Such a mine of information is value for money even though the cost is sixty shillings, but for this sum, the book should be better bound to withstand the frequent usage it deserves.

W. D. GRADDON

Principles of Fungicidal Action. By James G. Horsfall. (New Series of Plant Science Books, Vol. 30. Waltham, Mass.: Chronica Botanica Co.; London: Wm Dawson and Sons, Ltd., 1956.) Pp. xx + 280, 16 text-figures, 7 illustrations. Price: U.S. $6.50.

This, as the preface states, is no 'cook book' for the use of fungicides, neither is it a replacement of the author's earlier *Fungicides and their action* (1945) from the same publishers. The primary emphasis of the earlier book was on the dosage-response curve as a tool to investigate fungitoxicity while that of the latest is 'on the mechanisms of toxicity and the types of compounds which produce effects'.

Such a book by Horsfall needs no commendation to students of plant protection and though specialists may find many details familiar they will welcome the assembling of a vast amount of data so compactly (the 28-page bibliography includes more than 600 references up to about 1954) and the lively presentation.

The book has, however, potentially another function. If, as the author states in the chapter on the effect of fungicides on the metabolism of the fungus, 'those dealing with fungicides have made little effort to integrate the researches on fungus nutrition with those on fungus poisons', the converse is also true. Students of fungal physiology have yet to consider the implications of many interesting facts discovered during researches on fungicides, and it would be impossible for anyone interested in the mechanisms of fungal

metabolism to look through this book without getting ideas for speculation and suggestions for topics which merit investigation.

Finally it may be noted that, in line with the Chronica Botanica tradition, attention is drawn to the deep roots (extending back to Homer) of this recent and major development in the plant sciences and it goes without saying that the book is well produced.

G. C. AINSWORTH

The Classification of Lower Organisms. By HERBERT F. COPELAND. (Pacific Books, Palo Alto, California, 1956.) Pp. 302, 1 plate, 45 text-figures. Price: U.S. $7.50.

Are fungi plants? Few of the increasing number of those who answer this question in the negative seriously consider the wider implications of their opinion. Some, following the lead of Prof. G. W. Martin, carefully avoid the application to fungi of terms such as 'saprophyte' which imply a plant-like nature but most remain traditionalists. Dr Copeland is both more radical and more consistent. In addition to fungi, he excludes algae (with the exception of the green algae) from the Plant Kingdom and considers that the protozoa should not be classified as animals. These excluded forms he arranges as two additional kingdoms: Kingdom Mychota (comprising a single phylum) for bacteria and the blue-green algae (which, it is considered, lack a nucleus) and Kingdom Protoctista (with eight phyla) for the remainder. Fungi (with the exception of the Oomycetes (which find a place alongside the brown algae), Archimycetes (phylum Opisthokonta), and Mycetozoa) comprise the phylum Inophyta in which the subordinate taxa closely resemble those currently employed.

Many of the changes advocated by Dr Copeland have already been proposed by others and no mycologist considers that the taxonomy of fungi has reached finality. At first glance, however, many readers may be shocked by the nomenclature adopted for even familiar taxa. Dr Copeland has coined few names but he has conscientiously applied the principle of priority in selecting the names he needed, with some surprising results. For example, Mucedines Fr. is applied to the Plectascales, the Pyrenomycetes are designated Sclerocarpa Pers., and Fungi, in the sense of Linnaeus, is restricted to those inophytes better known to-day as the Agaricales.

These nomenclatural aberrations must not obscure a sincere attempt to solve a current problem and the author should rather be congratulated on a courageous and provocative book.

G. C. AINSWORTH

The Genus Phytophthora. *Diagnoses (or Descriptions) and Figures from the Original Papers.* By GRACE M. WATERHOUSE. (Miscellaneous Publication No. 12. Commonwealth Mycological Institute, Kew, 1956.) Pp. 120, 77 figures. Price: 15*s*.

This publication is both useful and novel. Every systematist appreciates the importance of original descriptions, the difficulties at times of consulting them, and the dangers inherent in accepting the word (which is so often the interpretation) of other workers as to their contents. All students of *Phytophthora*, and there are many, will therefore welcome this compilation in which the original descriptions of all the species which have been classified in *Phytophthora*, and the eight genera now placed in synonymy within it, are reprinted together with translations (if in a language other than English) and any illustrations. The text is reproduced by lithoprinting from an I.B.M. typewritten MS. and photostats or photographs of the original figures. One blemish of the workmanlike format, but easily remedied with a pen, is the absence of a title from the spine.

G. C. AINSWORTH

Tobacco Diseases with Special Reference to Africa. By J. C. F. Hopkins. (Commonwealth Mycological Institute, Kew, 1956.) Pp. xvi + 178, 57 plates (5 in colour), 7 text-figures. Price: 35*s*.

This is a much needed book which sets out in simple terms a great deal of useful information about diseases of tobacco in Africa. The author is well qualified for his task, having spent most of his professional life in Southern Rhodesia and worked with and written extensively about the diseases of tobacco. It is in no sense an academic book to read by the fire; there is no elaborate history of tobacco in the introduction nor is there a comforting chapter on the economic losses caused by disease, to justify the book's existence. The author knows from experience the losses caused and after a short chapter on 'The nature of disease', plunges straight into a discussion of 'Care of seed-beds and plant hygiene', a section of some 46 pages, calling on a great deal of first-hand experience. Then follow sections on parasitic diseases in seed-beds; parasitic diseases in the field; miscellaneous diseases and disorders; and curing diseases. In these sections the diseases of tobacco are dealt with in considerable detail, attention being given to specific control measures which, in the author's experience, have worked. A considerable interest attaches to the comparison between tobacco diseases in Africa and America. This is the first comprehensive and readily available account of tobacco diseases in continental Africa and as such it throws into perspective the relative importance of different diseases in the two continents. It is possible that some, especially professional plant pathologists, might consider that there is some unnecessary information in the book and that simple points are repeated more than is necessary, but the author has tried to write down his own experience and to include such information as he has had to seek when engaged with diseases in the field. As such he has made a valuable contribution and any general pathologist faced for the first time with African tobacco diseases will find the book of great utility. The book is well produced and the coloured and half-tone plates are useful and of good quality.

N. F. ROBERTSON

Bibliographie der Pflanzenschutz-Literatur: 1950. By J. Bärner. (Berlin: Paul Parey, 1956.) Pp. xli + 438. Price: DM. 42.

This Bibliography of Plant Protection is in continuation of the valuable series initiated by Prof. Morstatt in 1921, which now comprises a bibliography of plant pathological literature covering the years 1914–45 and 1950–1. The present compilation includes more than 13,300 titles for 1950 alone. Dr Bärner promises that the gap from 1946 to 1949 will be closed by the issue of further volumes going backwards to cover this intermediate period. One cannot fail to be impressed by the scope of this undertaking, nor by the courageous way in which Dr Bärner has restarted it, and is preparing to regain time stolen by the aftermath of war. The Introduction, Table of Contents and main headings throughout are given in English and French as well as in German, but the arrangement of this Bibliography is so well planned that this refinement is a luxury for the unlettered reader. After a short general section, the second section covers the causes of disease and poor growth in crops (general, undetermined, non-parasitic, micro-organisms, phanerogamic parasites, weed competitors, animal parasites, and viruses), the third and longest section covers diseases arranged by host plants, and the fourth section is concerned with plant protection. Both Dr Bärner and his publishers are to be congratulated on the present volume, and all plant pathologists will wish them good luck in their efforts to close the gap in this valuable series.

S. D. GARRETT

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CONTENTS

PAGE

Presidential Address. Approach to Discomycetes. By W. D. Graddon. (With portrait) 1

Studies on soil chytrids. II. On *Karlingia dubia* Karling. By L. G. Willoughby. (With 5 Text-figures) 9

The genus *Paecilomyces* Bainier and its perfect stage *Byssochlamys* Westling. By Agnes H. S. Brown and George Smith. (With Plates 1 and 2, and 16 Text-figures) . 17

Three leaf diseases of young oil palms associated with *Helminthosporium* spp. By W. G. Kovachich. (With Plate 3 and 3 Text-figures) 90

Studies on *Pellicularia filamentosa* (Pat.) Rogers. II. Occurrence and distribution of pathogenic strains. By N. T. Flentje and H. K. Saksena. (With Plate 4) . 95

Zygospores in *Piptocephalis*. By G. Leadbeater and C. Mercer. (With Plate 5 and 1 Text-figure) 109

Studies of British species of *Endogone*. I. Morphology and taxonomy. By Rosemary M. Godfrey. (With Plate 6 and 3 Text-figures) 117

Studies of British species of *Endogone*. II. Fungal parasites. By Rosemary M. Godfrey. (With 1 Text-figure) 136

Some effects of pea root exudates on physiologic races of *Fusarium oxysporum* Fr. f. *pisi* (Linf.) Snyder & Hansen. By E. W. Buxton. (With 4 Text-figures) . . 145

Heliscus stellatus sp.nov. An aquatic hyphomycete. By C. T. Ingold and Vivienne J. Cox. (With Plate 7 and 2 Text-figures) 155

British Records, 13 159

1947–1956 161

Proceedings 164
The Flatford Mill Foray, 1956 169
The Thirtieth Annual Plant Pathology Field Meeting 173

Reviews 174

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The standards adopted in the *Transactions* are those outlined in the Royal Society's pamphlet, *General Notes on the Preparation of Scientific Papers* (1950, The Royal Society, Burlington House, London, W. 1, price 2*s*. 6*d*.). An exception is that in the *Transactions* citations of references to literature, although based on the Harvard system, include the full titles of the papers and complete page numbers. Titles of journals are abbreviated in accordance with *A World List of Scientific Periodicals*, 1952.

The scientific names of genera and species are printed in italics and should be underlined in the typescript. The title of the paper, headings, and subheadings may be in capitals, but should not be underlined.

The attention of authors proposing new taxonomic groups is drawn to the need to give adequate descriptions and figures, and to designate the types as required by the *International Code of Botanical Nomenclature*. The description of a new species should be accompanied by a figure, and whenever possible the type specimen should be deposited in one of the national herbaria.

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